ASPECTS OF THE ECOLOGY OF INSECTIVOROUS BATS (CHIROPTERA) IN TEMPERATE DECIDUOUS WOODLANDS

by

Niamh Roche B.Sc.

A thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

University of Warwick

Institute of Education, Environmental Sciences and Education Research Unit

June 1997

And suddenly there was a terrible roar all around us and the sky was full of what looked like huge bats, all swooping and screeching and diving around the car, which was going about a hundred miles an hour with the top down to Las Vegas. And a voice was screaming: "Holy Jesus! What are these goddamn animals?"

H.S. Thompson (1971)

Table of Contents

Chapter 7: THE RELATIONSHIP BETWEEN BAT PASSES AND BAT DENSITY: A COMPUTER SIMULATION

List of Tables

List of Figures

Acknowledgements

Thanks to my supervisor, Paul Elliott for his help and encouragement. Also to colleagues in Science Education and thereabouts, in particular: Sue Barker, Richard Beare, Brian Ellis, Eddie Gray, Don Kelly, Jim Littlemore, Barry Meatyard, Sue Podmore and Brian Tustin. I am grateful to Craig Emms, Nigel Raine, members of Warwickshire Bat Group and others who helped with field work. Thanks also to Warwickshire Biological Records Centre and Bablake Weather Centre for kindly providing information and data, and land and roost owners for access to their properties. I am also grateful to Colin Catto of the Bat Conservation Trust for advice and helpful comments and fair play to Cormac Parle for his contribution to the Batmodels. This research was financed by the University of Warwick.

Thanks to all my friends in Britain and in Ireland for their support during the past four years. Special thanks to Corm and my family.

Declaration

I declare that the work presented in this thesis has not been submitted for a degree at any other University. This work has not been published, except for an amended version of Chapter 3 (questionnaire survey) which will be published in a special edition of *Myotis* as Proceedings of the VIIth European Bat Research Symposium.

I also declare that I am the sole author of this thesis.

Summary

Ecological requirements of temperate bat species have been the subject of research in recent years. Remaining native woodlands are believed to be particularly important as foraging sites for bats in Britain. However, little work has been conducted on these habitats.

This thesis examines spatial and temporal variations in bat activity in woodlands in relation to a number of factors including prey availability and diversity, weather variables and vegetation density.

In this thesis, preference or avoidance of a woodland microhabitat was found to be related to vegetation density of the shrub and canopy. Optimal microhabitats balance the requirements for openness (related to a bat's morphology and echolocation capabilities) and a degree of shelter (necessary for predator avoidance).

Nocturnal activity of *Pipistrellus pipistrellus* in woodlands was investigated and where the woodland was situated in close proximity to a roost, activity was unimodal during pregnancy, bimodal during lactation, and unimodal after weaning. However, in one woodland where no maternity roost was found close-by, nocturnal activity patterns differed.

Seasonal bat activity within woodlands was examined in relation to insect availability and climatic factors. Activity was found to be mainly influenced by insect availability. The weather variables regulating insect abundance vary between woodlands and may largely be a function of site characteristics. The range and diversity of available prey taxa rarely affects activity of *P. pipistrellus*, the most commonly encountered bat in this study.

Bat detectors have been used in many habitat and landscape studies (including this one) to estimate bat activity. Until now, no direct association has been made between the number of bat passes and the density of bats present. This issue was investigated using computer simulation models. A nonlinear relationship was found between bat passes and bat density, reducing to an almost linear relationship at the low bat pass numbers typically found in the field.

List of Abbreviations

abund. = abundance

ave. = average

bar. = barometric

BWS = Bablake Weather Station, Coventry

corr. = correlation

DWLS = Distance weighted least squares smoothing

humid. = humidity

Long Itch = Long Itchington Wood

M = no. of variables included in correlation analysis

max. = maximum

min. = minimum (in Chapter 5)

Myo. = *Myotis* species

p = probability

P. pip. = *Pipistrellus pipistrellus*

pref. = preferences

press. = pressure

rel. = relative

Rough = Roughknowles Wood

sec. = seconds

sign. = significant

temp. = temperature

veg./ vegetat. = vegetation

WBRC = Warwickshire Biological Records Centre, Warwick.

+ve = positive correlation between two variables

-ve = a negative correlation between two variables

* = significant at a 10% level

** = significant at a 5% level

*** = significant at a 1% level

Chapter 1

INTRODUCTION

1.1 Bat diversity, distribution and roost location

1.1.1 Diversity and distribution

There are approximately 970 known bat species (Corbett and Harris, 1991) and they are divided into two suborders: the Megachiroptera, and the Microchiroptera. The Megachiroptera feed mainly on fruit and other plant substances and the Microchiroptera eat a wide variety of food including: fish, pollen, nectar and insects (Corbet and Harris, 1991).

Megachiroptera are found mainly in tropical and subtropical regions where the diversity of bat species is greatest (Findley, 1993). Although the Microchiroptera have exploited all major land habitats, in cool temperate regions, species are fewer (Findley, 1993). The 14 or so species of bat resident in Britain (Stebbings, 1993) are all insectivorous Microchiroptera. Twelve of these belong to the family Vespertilionidae and the remaining two to the family Rhinolophidae (horseshoe bats). All can use high frequency sounds in echolocation to avoid obstacles and to capture prey (Stebbings, 1993). The most diverse range of species is found near the south coast (Corbet and Harris, 1991), while to the north of Scotland, breeding populations are found among only four species (Stebbings, 1993).

Evidence for species distribution changes has been provided from cave remains. For example, Neolithic remains of *Rhinolophus hipposideros* (lesser-horseshoe bat) have been found in Dowel Cave, Derbyshire, a region where the lesser-horseshoe bat is no longer present (Yalden, 1968). More recently, bat conservation has become an important issue (e.g. Fenton, 1992; Kunz, 1988; Stebbings, 1988; Stebbings, 1993), with a decrease in the availability of foraging habitat one of the main reasons attributed to their recent decline (Racey and Stebbings, 1972; Stebbings, 1988).

Warwickshire is a county in central England in which 11 bat species have been recorded (WBRC). However, few roosts are known, despite a relatively suitable landscape of agricultural land and interspersed woodlands.

1.1.2 Roost location

Locating roosts is important because the abundance and location of roosts can be used as an indicator of species' population status and can provide information about species' conservation requirements (Sargent, 1995).

Various methods have been used to locate roost sites including: radio telemetry (e.g. Kronwitter, 1988), ultrasonic detector surveys (e.g. de Jong and Ahlén, 1991) and poster campaigns (e.g. Speakman *et al.*, 1991).

Radio telemetry involves attaching a small battery powered, pulsed signal, radio transmitter of known weight to a bat using an adhesive (Barclay and Bell, 1988). The bat's movements can then be tracked using a receiver with directional antennae. Radio telemetry is an expensive method for locating roosts (Barclay and Bell, 1988).

Bat detector surveys involve monitoring bat movements at dusk and dawn and exploit the fact that many species use defined flight paths along linear landscape features when commuting between roosts and feeding sites (see Limpens, 1993). With a high level of co-operation among field workers it is possible to back-track along a flight path and locate roosts (Limpens, 1993). Although this method is relatively inexpensive, it requires intensive manpower.

A poster campaign has been used by Speakman *et al.* (1991) in Scotland to locate roost sites. However, although central England is relatively densely populated, the community is largely dormitory with few shops, public houses or other foci for community life. This negates the use of posters to locate roosts.

In Chapter 3 a novel method is described for locating bat roosts using a questionnaire survey.

1.2 Bat activity

1.2.1 Climate

The influence of climate on bat activity has been the focus of several studies. Flight activity of bats generally increases with temperature (e.g. Catto, Racey and Speakman, 1995; Negraeff and Brigham, 1995). Flights are of shorter duration on cooler nights (Anthony, Stack and Kunz, 1981) and extended on warmer nights (O'Farrell, Bradley and Jones, 1967). Catto *et al.* (1995) found that minimum ambient temperature was correlated with the amount of time *Eptesicus serotinus* (the serotine bat) spent away from the roost. Ambient temperatures below 10°C were associated with a reduction in activity.

Relative humidity may have an important effect on bat activity. Adam, Lacki and Shoemaker (1994) found decreased activity with lower humidity. Bats lose water during flight and possibly in roosts (Carpenter, 1969). Some species have evolved water balance mechanisms adapted to their lifestyle: for example, *Myotis daubentonii* (Daubenton's) feeds primarily over water (Corbet and Harris, 1991; Swift and Racey, 1983). This species is often found occupying the same roost as *Plecotus auritus* (brown long-eared bat) but the two differ in other aspects of their water balance (Webb, Speakman and Racey, 1994). There is high post-prandial urine loss in *M. daubentonii*. This may be an adaptation to enable disposal of excess water taken in when foraging (Webb *et al.*, 1994). In the roost, evaporative water loss is greater in *P. auritus* than in *M. daubentonii*. Daubenton's bats have a physiology preventing excess water loss when at rest within the day roost compared to *P. auritus* under equivalent conditions (Webb *et al.*, 1995).

Rainfall is another climatic variable which may modify bat activity. Erkert (1982) noted that many species are reluctant to fly in heavy rain. However, Catto *et al.* (1995) found no relationship between rainfall and activity of *E. serotinus*.

Some bat species show reduced activity in windy conditions (O'Farrell *et al.*, 1967; Adam *et al.*, 1994). Barometric pressure may also affect activity. Paige (1995) found a negative relationship between activity and barometric pressure.

1.2.2 Prey availability

Rautenbach, Kemp and Scholtz (1988), noted that certain weather variables (e.g. rainfall, temperature and relative humidity) through their effects on prey availability, affect the activity and breeding patterns of insectivores such as bats. Rautenbach *et al.* commented that the importance of differential food availability had been understressed among researchers.

Patterns of nightly bat foraging activity often peak immediately after dark and before dawn (e.g. Fenton, 1970; Kunz, 1973, 1974; Swift, 1980), correlating with times of maximum insect availability. Overall activity within habitats often positively relates to insect abundance (e.g. Racey and Swift, 1985; Rautenbach *et al.*, 1988; Rautenbach, Fenton and Whiting, 1996).

In temperate zones, the timing of bat reproductive cycles are based on availability of an adequate food supply, particularly around the time of lactation and weaning (Racey, 1982). Fertilisation, implantation of fertilised eggs and foetal development can all be delayed in order to synchronise lactation with high prey abundance (Racey, 1982). Experiments with pipistrelle bats have shown that gestation length depends on temperature and food supply during pregnancy. When palpably pregnant bats were deprived of food in a cold environment (5, 10 and 11 to 14°C), they became torpid and

pregnancy was lengthened by a period similar to that of the induced torpor. This indicated that foetal development was arrested (Racey, 1973).

Metabolic rates among pregnant *Myotis lucifugus,* a temperate bat, decreased by 61%, and lactating *M. lucifugus* by 46%, following a day of food deprivation (Kurta, 1991).

In Chapter 6 climate and insect availability are examined to determine which plays a greater role in influencing seasonal bat activity in woodlands and woodland microhabitats.

1.2.3 Moonlight

Moonlight may influence bat activity. However, reports on its effects have been somewhat contradictory. The neotropical fruit bat *Artibeus jamaicensis* has been described as lunar phobic because it exhibits interrupted feeding activity during nights around the full moon, while around the new moon foraging continues from dusk until dawn (Morrison, 1978).

Scotophilus borbonicus, an African bat studied by Fenton and Rautenbach (1986), foraged at high levels around the canopy or around the edges of woods or clearings but hunted below the canopy on bright moonlit nights.

Negraeff and Brigham (1995) found no lunar cycle influence on activity of *M. lucifugus.* The authors hypothesised that should *M. lucifugus* be truly lunar phobic, activity would shift to more sheltered habitats during the full moon. However, they found no evidence of a habitat shift correlated with lunar light levels. In contrast, Adam *et al.* (1994) found a negative relationship between flight activity of *Corynorhinus* (previously *Plecotus*) *townsendii virginianus* and moon phase.

In order to negate any possible influences of the lunar cycle on insect (section 1.3.4) or bat activity, field work for this research was carried out during the new, and between the new and full moons, in 1995. In 1996, field

work was carried out irrespective of stage of lunar cycle and this factor was taken into account during analysis (see Chapter 6).

1.2.4 Nocturnal activity patterns

Nocturnal bat activity is determined, at least partly, by weather and its effects on insect availability. Energetic advantages are probably derived from night roosting when cool ambient temperatures and low insect densities prevent net energy gains from foraging (Anthony *et al.*, 1981).

However, reproductive state is also a factor influencing activity patterns during the night. Nocturnal activity of *E. serotinus* in England was examined by Catto *et al.* (1995) by counting the number of individuals emerging from the roost. Activity was found to be bimodal during mid- and late-pregnancy and intermittent returns were made to the roost during lactation. Similar behaviour was recorded for *E. serotinus* in Denmark (Degn, 1983).

Pipistrellus pipistrellus (the pipistrelle) exhibits unimodal patterns of activity during pregnancy and bimodal patterns during lactation, in Scotland (Swift, 1980; Racey, Speakman and Swift, 1987), and England (Maier, 1992). Swift's (1980) study showed that these peaks during lactation and weaning coincided with peaking insect densities at dusk and dawn.

Patterns of activity around the roost may be reflected during the night in woodlands where bats are active. *P. pipistrellus* activity during the night was determined using ultrasonic detectors along transects in study woodlands. In Chapter 5, activity patterns are compared with insect availability and with previous work on nocturnal activity patterns.

1.2.5 Morphology and echolocation

Some species of bat exploit a combination of different foraging habitats (e.g. *P. pipistrellus*, Rydell *et al.*, 1994; Vaughan, 1996) although some use

single habitat types (e.g. *P. auritus,* Entwistle, Racey and Speakman, 1996). The type of area available to forage in is a function of a combination of morphological and echolocation characteristics (Norberg and Rayner, 1987). Neuweiler (1990) summarised habitat use by bats in relation to wing morphology and acoustic characteristics. There is a spectrum of morphologies ranging from species with long narrow wings foraging above vegetation (fast-flyers), to gleaners which pick up prey from a surface and generally have short broad wings which enable hovering.

Echolocation calls also determine potential foraging sites for a species. Fenton and Rautenbach (1986), in a comparison of three species of insectivorous bat, noted that each used echolocation calls which reflected their ability to deal with clutter. Gleaners often have low intensity echolocation while fast fliers echolocate loudly (Neuweiler, 1990).

There is little interspecific competition in a bat community because each species has a different combination of auditory and flight capabilities (Norberg and Rayner, 1987; Neuweiler, 1990; O'Neill and Taylor, 1989).

Some bat species, because of their morphology and echolocation, may be unable to fly in densely vegetated woodland microhabitats. This issue is discussed in greater detail in section 1.5 and in Chapter 4.

1.2.6 Estimating bat activity

There are many different types of bat detector available to researchers. These include: envelope detection instruments (broadband), frequency division (also broadband), heterodyne (narrowband) and time expansion (broadband) detectors (Pettersson, 1993).

Ultrasonic detectors have been widely used for monitoring general bat activity (Fenton and Bell, 1981; Fenton, Merriam and Holroyd, 1983; Thomas and La Val, 1988), and are particularly useful when examining threatened species, because the method is non-intrusive (Fullard, 1989). Both narrow-

band and broadband ultrasonic detectors have been used to detect bat activity and indicate habitat use and distribution (e.g. Blake *et al.*, 1994; Fenton *et al.*, 1983; Fenton, Tennant and Wyszecki, 1987; Fullard, 1989; Furlonger, Dewar and Fenton, 1987; Navo, Gore and Skiba, 1992; Tangney and Fairley, 1994; Vaughan, 1996; Walsh, Harris and Hutson, 1995).

According to Thomas and La Val (1988), *"bat detectors provide no more than a relative index of activity because there is no one-to-one correlation between bat passes and the number of individuals present"*.

Using a computer model of simulated bats moving through a 2-dimensional plane, the hypothesis that there is no correlation between bat passes and the number of bats present is examined in Chapter 7.

1.2.6.1 Heterodyning

A tuneable heterodyne detector was chosen for field work. These instruments are reliable and cost efficient. Tuneable detectors generally pick up a small window of sound on either side of the frequency tuned to (±8kHz for Bat Box III) (Jones, 1993). This means that characteristics of the sounds of echolocating bats can be determined to a limited extent, for example the 'smacking' noise produced by the CF (Constant Frequency) tail of *P. pipistrellus* calls can be heard and the 'ticking' of the FM (Frequency Modulated) *Myotis* spp. calls (Catto, 1994). The detector can be tuned up and down to determine the lowest/highest signal frequency (Pettersson, 1993): this is sometimes characteristic of species and can aid identification. The Bat Box III is most sensitive to sounds at 40kHz (Jones, 1993).

1.2.6.2 Disadvantages of heterodyning

A disadvantage of using a heterodyne detector is that echolocating bats at other frequencies (e.g. when tuned to 45kHz, the *Rhinolophus, Eptesicus* and *Nyctalus* spp.) are often missed. Also, it is only rarely possible to pick up very

quietly echolocating bats (e.g. *P. auritus*, Ahlén, 1990; Corbet and Harris, 1991).

Some species do not echolocate when attempting prey capture by gleaning (Anderson and Racey, 1991; Faure, Fullard and Barclay, 1990). Anderson and Racey (1991) found that captive *Plecotus* made more successful capture attempts on stationary moths when they did not use echolocation signals at all. A similar vespertilionid bat *Myotis evotis* only uses echolocation during 59% of attacks on stationary moths, suggesting the bats use passive listening as an important component of foraging (Faure *et al.*, 1990).

Loudly echolocating bats are recorded more often than quiet bats. Intense echolocators include: *P. pipistrellus, Myotis mystacinus /brandtii* (whiskered/Brandt's) and *Nyctalus noctula* (the noctule) (Stebbings, 1993). Because some species are more easily detected than others, no direct comparisons can be made of activity between species (Thomas and La Val, 1988).

Bats can change the structure of their call according to the situation they are in. An echolocating bat which is approaching a target will shorten its pulses and increase its bandwidth emissions, sometimes by the addition of harmonics (Fenton, 1986). When bats are flying close to the ground or near obstacles search pulses are short, of high frequency and large bandwidth and when the bats fly high in open space the calls are of long duration, small bandwidth and low frequency (Zbinden, 1989). Thus some species flying in clutter may change their calls: for example *P. pipistrellus* shorten the CF portion of their calls in closed habitats, thus rendering discrimination between pipistrelles and *Myotis* spp. more difficult (Catto, 1994).

1.2.6.3 Bat activity observations

Attempts have been made by some authors to distinguish between the search, approach and terminal phases ("feeding buzz") of a bat pass in order

to distinguish foraging and non-feeding bats (e.g. Rydell *et al.*, 1994). However, bat passes alone are considered sufficient as estimates of activity in this study. Walsh *et al.* (1995) found a strong correlation between bat passes and number of feeding buzzes.

Activity estimates can be made either by observing the number of bat passes at one point (e.g. Ahlén 1980-81; de Jong 1994; Tangney and Fairley, 1994) or by walking transects of known length (e.g. de Jong, 1994; Walsh *et al.*, 1995). Measuring bat activity by observing bat passes at one point for a length of time may be more susceptible to errors than walking a transect several times because at one point there is a possibility that the same bat is being observed repeatedly. This risk may be lessened when the surveyor is moving. In other words, the probability of recording high activity on a transect as a result of a rapidly circling bat on a small beat may be lower than when estimating activity at a single observation point. A large number of observation points are, in effect, similar to a line transect.

1.2.7 Species expected using a detector survey

Some bats are not expected to be commonly observed in woodland, for example *M. daubentonii*(due to its preference for foraging over water habitats (Corbet and Harris, 1991)). Species rarely recorded in Warwickshire, for example *Myotis nattereri* (Natterer's bat) and *R. hipposideros*, are also not expected frequently.

P. pipistrellus is the bat species most likely to be encountered during activity observations in this study because it is the species most commonly recorded in Warwickshire (WBRC). Two phonic types of the common pipistrelle have recently been distinguished which have mean echolocation frequencies of maximum energy at 55kHz and 46kHz (Jones and Van Parijs, 1993). These two types are commonly known as the 55kHz and 45kHz types for simplicity. They are likely to be two sibling species (Barratt *et al.*, 1995).

P. pipistrellus is predicted, from morphological measurements, to be a fast flier for its size (forearm<35mm, Corbet and Harris, 1991) (Baagöe, 1987). The two phonotypes have similar wing structure and morphology, however some differences have been found in their preferred foraging habitat. Vaughan (1996) found that the 45kHz type foraged in many habitats including rivers, lakes and woodland, while the 55kHz type fed mainly over rivers and lakes.

In Warwickshire, no distinction has been made to date between the two phonotypes, so relative abundance of the two is unknown. However, given that the 45kHz type has been noted in woodlands elsewhere in Britain, it may be more commonly encountered during this study than the 55kHz type (see Chapter 4, Results).

M. mystacinus/brandtii (whiskered/Brandt's) are sibling species both of which are found in Warwickshire (the whiskered may be more common). These two species are indistinguishable using a heterodyne bat detector. They may also be commonly detected in a woodland survey (see section 3.1.3)

1.3 Insect abundance

In Chapter 6 abundance of insects is examined in relation to *P. pipistrellus* and *Myotis* spp. activity.

1.3.1 Diurnal and seasonal periodicity

There is a peak in aerial insect abundance during the first two hours after sunset (Mayle 1990a), which is often utilised by foraging bats. Lewis and Taylor (1964) reviewed the diurnal periodicity of insects. Night flight is more common among Diptera (Nematocera), Lepidoptera, Neuroptera and Trichoptera, than other taxa. Lewis and Taylor (1964) observed that light

intensity is a crucial factor determining flight of different species and that flight is also seasonal.

Williams (1939), in his study of four years' catches in a light trap (Rothamsted, England) found that numbers of taxa peaked during the warm mid-summer months. Seasonal distribution of insects has also been demonstrated by Yack (1988) when he found that atympanate (deaf) moths were found in greatest abundance during parts of the summer when bat numbers are lowest and by Davis (1983) with a study of invertebrates associated with nettles (*Urtica dioica*). Certain species have peaks in abundance once or twice during the year and different species emerge during different months.

1.3.2 Spatial distribution

Insects are often unevenly distributed in space. Peng, Sutton and Fletcher (1992) showed that most dipteran families were found in greatest concentration close to an emergent hedgerow tree, although some families (Diptera: Scatopsidae) were found in large numbers away from the tree. Vertical distributions of dipterans were also, to some extent, family specific. Williams (1939) noted that the light trap caught several species of Noctuidae (Lepidoptera) at a height of 10.6m which were absent or rare in the trap at approximately 1m.

1.3.3 Climate

A combination of different weather variables influence insect abundance (Rautenbach *et al.*, 1988; Williams 1940; Wellington, 1945). Temperature is particularly important: fewer insects fly in low temperatures (Taylor, 1963; Williams, 1940; Wellington, 1945).

There has been some controversy over the findings of authors regarding other weather variables, for example Wellington (1945) dismissed

relative humidity as an important factor influencing aerial insect activity while Peng (1991) found that several dipteran families flew more readily in dry conditions. Wellington (1945) also rejected barometric pressure as a factor affecting flying insects while Paige (1995) found a negative correlation between insect abundance and pressure.

Weather variables also influence insects among vegetation. In England where *Aedes cantans* (Diptera: Nematocera) normally rested amongst vegetation, numerous adults were found in rodent burrows during an exceptionally dry period. The burrows were left again after heavy rain (Service, 1973a). Rain was also shown to affect numbers of resting *Culex nigripalpus* (Diptera: Nematocera) in Florida. Gravid females were observed to have a negative association with daily rainfall during the wet season from July onwards (Day, Curtis and Edman, 1990).

1.3.4 Moonlight (see also section 1.2.3)

Moonlight is an important factor influencing insect activity. The indirect effect of moonlight in insect trap catches has been well documented (Bidlingmayer, 1964). A number of authors have noted a reduction in collection sizes during full moon periods of the lunar cycle compared with new moon periods (Bradley and McNeel, 1935; Horsfall, 1943; Pratt, 1948; Provost, 1959). The reason for lower catches is the reduction of effectiveness of UV light as an attractant due to the much higher ambient light levels on a full moon night (Bidlingmayer, 1964).

Although moonlight can cause an overall reduction in light trap catches, it can increase the numbers of flying female mosquitoes significantly. Bidlingmayer (1964) found that female *Aedes taeniorhynchus* numbers increased by 546% during the full moon. Bidlingmayer observed that light intensity of the full moon is close to that of twilight when most flight activity occurs.

Anderson (1966) suggested that feeding and various activities among insects associated with low light intensities, may have evolved to avoid predation from visually oriented predators.

1.3.5 Predator avoidance

Avoidance tactics by aerial insects are likely to affect their availability to preying bats. Many insects which are relatively common in aerial fauna have evolved mechanisms to avoid predation. Evasion tactics are known in members of four insect orders: Lepidoptera, Orthoptera, Dictyoptera (preying mantids) and Neuroptera (Miller and Surlykke, 1995). Some Arctiidae (Lepidoptera) are thought to be distasteful to bats (Thompson, 1982) and emit ultrasound clicks which are said to jam bat echolocation sequences (Fullard, Simmons and Saillant, 1994).

Acharya (1992) noted that moths with ears successfully avoided predating *Lasiurus borealis* and *L. cinereus* about 40% of the time, while deafened moths of the same families were caught more often on bats' first attacks.

Lewis, Fullard and Morrill (1993), studied earless Lasiocampidae moths in a Nearctic site and found that some species had peak emergence times mismatched with those of bats. Also, many earless species flew close to the ground and more erratically than eared species.

1.3.6 Estimating insect abundance

Most methods of trapping and catching insects are biased in some way (e.g. Southwood, 1978; Kunz, 1988) and it is only by combining several techniques that a good overall estimation of invertebrate communities can be made. There are two categories of insect trap: those which trap aerial insects, and those which catch resting and aerial insects.

1.3.6.1 Aerial insect traps

Aerial insect traps may be attractant or non-attractant. The best known of the non-attractant traps are the Johnson-Taylor suction trap (Johnson 1950, Taylor 1951, Johnson and Taylor 1955) and the Rotary or Whirligig trap (Kunz, 1988).

The Johnson-Taylor suction trap is frequently used to assess aerial insect densities and can segregate catches from every hour. The efficiency of this trap is affected by wind speed and fan performance (Taylor, 1962). Johnson-Taylor suction traps have been used in prey availability studies by many authors (e.g. Anthony *et al.*, 1981; Racey and Swift, 1985; Swift *et al.*, 1985). The suction trap is the only trap which can give reliable estimates of both absolute and relative density (Hollyfield, 1993) (relative density was considered sufficient for this study).

The rotary trap can be used to estimate the numbers and density of airborne insects by moving one or more nets through a fixed air space at a constant speed (Kunz, 1988). The efficiency of the rotary trap is independent of windspeed until the speed of wind exceeds the speed of the trap (Kunz, 1988). Both suction and rotary traps require a source of power - either mains or generator.

The rotary trap is biased against trapping larger beetles (Juillet, 1963) as are suction traps (Southwood, 1978). However, despite this skewing, Brigham and Saunders (1990) recommend the use of more than one insect sampling device including either a whirligig or suction trap when carrying out insect availability studies.

Other non-attractant traps for sampling aerial insect population include: tow nets, malaise traps, impaction traps and sticky traps.

Tow nets are attached to a vehicle and it possible to control the volume of air sampled by maintaining a known vehicle speed while covering a

transect. Nets can be attached to any moving vehicle (McClure, 1938; Karg, 1980; Steelman *et al.*, 1968; Reling and Taylor, 1984).

Malaise traps (Malaise, 1937) catch airborne insects and consist of netting which insects crawl or fly into (Gresitt and Gresitt, 1962). Simple design means it can be used in a wide range of habitats. Juillet (1963) showed that Malaise traps caught relatively few insects and were biased against trapping coleopterans and hemipterans.

Impaction traps capture flying insects when they hit a hard surface and fall, stunned, into a container. Most of these traps are constructed using glass or plexiglass plates (Service, 1993; Southwood, 1978). A limitation is that they tend to be highly directional (Kunz, 1988).

Aerial insects adhere to sticky traps upon contact (e.g. Service 1976; Southwood, 1978). Trapping efficiency is affected by wind because insects may be flushed in one direction (Kunz, 1988). Juillet (1963) observed that sticky traps are inefficient at catching large insects and they catch smaller ones than the Malaise trap.

Attractant traps are those which interfere with an insect's sensory orientation or movements and are used by entomologists for general collections (Southwood, 1978). These traps include pheromone and light traps with light traps being the type most commonly used.

A light trap's radius or catchment area is affected by the contrast between light from the trap and ambient light in the surroundings (Kunz, 1988). Moonlight can have an effect on catchment area size (Bowden, 1973; 1982) (see section 1.3.4). Bowden and Morris (1975) suggested that the use of traps should be corrected for phase of the lunar cycle and intensity of moonlight throughout the night. Responses to light traps vary according to invertebrate taxa and sex. Moths (Lepidoptera) and caddisflies (Trichoptera) are more strongly attracted to mercury vapour than to UV lights (Kunz, 1988).

1.3.6.2 Resting populations

Resting populations can be estimated using nets (hand or sweep), fog or aspirators. Small hand nets can be used to capture insects by walking through vegetation and catching those that fly out. Good illumination is necessary and the method is not easily standardised (Service, 1993).

The volume of air sampled by a sweep net has, however, been quantified by Tonkyn (1980). Relative densities of different species resting in and around different types of vegetation and changes in densities associated with different times of the day or year can be obtained if the collecting technique is standardised and a known number of sweeps are taken. Many insects rest among grassy and shrubby vegetation and on tree foliage. In the U.S., Copeland (1986) caught mosquitoes from a wood by disturbing vegetation with a stick and collecting them with a sweep net. Some species may not be readily flushed out but can be caught if the vegetation is vigorously sweep netted (Service, 1993). Sweep netting has been used in England to study the distribution of mosquitoes resting in various types of vegetation (Service, 1971).

Fogging is carried out by spraying insecticides into the vegetation and canopy - insects which would normally be resting or feeding there can be collected (Service, 1993). A sheet of plastic is laid out on the ground and fallen insects preserved (Kay, 1983; Simmons *et al.*, 1989). This method of collection, although robust and complete, is very destructive.

Aspirators are divided into two groups; oral aspirators (e.g. Pooter), and mechanical aspirators. Oral aspirators are laborious to use and quite inefficient (Service, 1993). This method is biased because the collector must see the specimen to collect it. Mechanical or battery operated aspirators are usually converted hand-held vacuum cleaners (e.g. Dell'uomo, 1967; Husbands and Holten, 1967; Sudia and Chamberlain, 1967). Many different adjustments can be made to the original mechanism for example replacing the

dust bag by lengths of rubber tubing (Service, 1993). This method, however, may cause damage to insects because of impaction (Service, 1993) and reaching higher vegetation is difficult.

1.4 Woodlands: sites of high bat activity

Landscape studies have highlighted several important habitat types (e.g. de Jong, 1994; de Jong and Ahlén, 1991; Rydell *et al.*, 1994; Tangney and Fairley, 1994; Walsh *et al.*, 1995; Walsh and Harris, 1996a&b; Walsh and Mayle, 1991). In Britain, these include broadleaved woodland and riverine or wet environments (Walsh *et al.*, 1995; Walsh and Harris 1996a).

De Jong and Ahlén (1991), in a study of a community of ten bat species in Sweden observed that riparian habitats were the most important areas during spring and early summer whilst insects were scarce elsewhere. De Jong (1994) focused less on riparian sites and found that open areas (e.g. agricultural land) were least favoured by foraging bats and habitats associated with broadleaved woodland were preferred.

Rydell *et al.* (1994) discovered that the abundance of *P. pipistrellus* and *M. daubentonii* differed significantly between woodlands, open farmland and ponds and rivers. *P. pipistrellus* were recorded most frequently around ponds and rivers, less frequently around woodland and occasionally over open farmland. *M. daubentonii* were almost exclusively found in riverine habitats.

Tangney and Fairley (1994) studied the habitat preferences of bats in the environs of Connemara National Park, Ireland. Activity was greatest at pools and rivers, second highest in woodlands and also high around roads lined with trees. Few bats were active over open habitats such as bogland or rough pasture.

Little work on ecology and habitat requirements has been carried out on woodlands, although it appears to be a crucial habitat for many bat species (Mayle, 1990 a&b).

1.4.1 Woodland microhabitat exploitation

Woodland provides a wide range of ecological niches for bats of different morphologies to exploit. Bat communities of woodland and forest have been investigated by several authors. Some have found a preference among certain species for specific microhabitats within woodland.

Crome and Richards (1988) described bats in an Australian rain forest as closed canopy or gap specialists or gap incorporators by monitoring activity and from morphological measurements. Also in Australia, Fullard *et al.* (1991) defined bat species as using closed, edge or open microhabitats from wing morphology, echolocation calls, and observations, although some interspecific overlap occurs. In southern Africa, Aldridge and Rautenbach (1987) outlined a similar division of microhabitat resources among insectivorous bats.

Kutt (1995), compared thinned, unthinned and old regrowth forest in Victoria, South Australia, and found highest bat activity in unthinned woodland.

In the U.S., Thomas (1988) and Thomas and West (1991) found that *Myotis* spp. were detected much more frequently in old growth stands of Douglas-fir (*Pseudostuga menziesii*) forest than in younger stands. However, feeding rates were very low and activity was confined to 15 minutes around sunset. The authors took this to suggest that old growth stands were mainly used for roosting.

Krusic *et al.* (1996) surveyed foraging and feeding activity of bats in White Mountain National Forest. They found that activity was concentrated

at trail and water edges and, within forest, activity was highest in overmature hardwood and regenerating stands of both hardwood and conifer.

1.4.1.1 Edges

In Chapter 4, activity at woodland edges is examined and compared with results from other woodland research. In several studies, edges have been the woodland microhabitats of greatest activity (de Jong, 1984; Furlonger, Dewar and Fenton, 1987; Walsh and Harris, 1996a). Furlonger *et al.* (1987) showed that of five sympatric species of insectivorous bat studied in Ontario, Canada none of the species were confined to one specific habitat type. Some showed a significant preference for particular habitat features including woodland edges and artificial lights.

Walsh and Harris (1996a) found strong selection for woodland edges, and edges were preferred to openings within woodlands. They suggested that this was due to an accumulation of insects on the lee side of a windbreak (Lewis, 1967; 1970).

De Jong (1994) found that edges were the woodland microhabitat most preferred by *P. pipistrellus* although this microhabitat was generally avoided by *M. mystacinus*. De Jong found a decrease in insect abundance from open to edge to densely vegetated areas. A preference among some species for edges may be a balance between predator avoidance (edges provide some shelter) and high prey availability.

Many small bat species fly along linear landscape features (such as hedgerows and tree-lines) when they move from roost to foraging sites (e.g. Krull *et al.*, 1991; Limpens and Kapteyn, 1991; Limpens *et al.*, 1989). This behaviour may be linked to orientation (e.g. Entwistle *et al.*, 1996; Limpens *et al.*, 1989), and to avoidance of avian predation, which may be a substantial cause of mortality among bats (Speakman, 1991). If activity at woodland edges is related to bats commuting along linear landscape features, then

higher activity at edges would be expected early in the evening, compared with later in the evening. This hypothesis is examined in Chapter 4.

In contrast to the above studies, Vaughan (1996), examined bat activity using a detector at woodland edges and compared activity there with activity inside woodlands. She found no significant difference in activity levels inside woodlands and along woodland edges.

1.4.2 Native deciduous woodland

In Britain, particularly in the English Midlands, landscape is characterised by a patchwork of hedgerows and agricultural land interspersed with small woodlands, often ancient in origin (Tasker, 1991). Native woodlands mainly exist as small fragmented patches (Spellerberg, 1992) less than 20ha in area (Peterken, 1991). Nonetheless, researchers in Britain have underlined the importance of remaining native woodland to bats (e.g. Entwistle *et al.*, 1996; Mayle, 1990 a&b; Walsh and Mayle, 1991; Walsh *et al.*, 1995; Walsh and Harris, 1996 a&b).

Walsh and Harris (1996a) found that semi-natural woodland was preferred to mixed or conifer woodland. These results were similar to those of Entwistle *et al.* (1996) for *P. auritus*. This preference is likely to reflect higher prey availability than in non-native coniferous plantations (Waring, 1988; 1989). Native woodland has the richest invertebrate fauna of any British habitat (Kirby, 1992). A woodland's complex structure compared with other more structurally simple habitats provides a wide range of potential niches for invertebrates (Kirby, 1992).

Native broadleaf tree species support (as food and shelter providing habitat) a wide variety of arthropod species (Kennedy and Southwood, 1984). Kennedy and Southwood (1984) compiled a list of insects associated with native trees; the two native oak species (*Quercus petraea* and *Q. robur*) are associated with a total of 423 species of phytophagous insects and mites. Ash

(*Fraxinus excelsior*), another of the canopy forming trees supports 68 and sycamore (*Acer pseudoplatanus*), introduced from mainland Europe, supports 43 (Kennedy and Southwood, 1984). The sites in this study are semi-natural with well developed canopies of mainly native tree species (in Tocil Wood there are large numbers of sycamore). However, in the case of the sycamore, the biomass of insect fauna associated with mature specimens can often rival that of native species (Kirby, 1992).

The understorey can also support a large invertebrate community. Among the important species are; bramble (*Rubus fruticosus* agg.), ivy (*Hedera helix*) (Kirby, 1992), and bracken (*Pteridium aquilinum*) (Lawton, 1976). A woodland with diverse vegetation and a range of structural features such as glades and rides is likely to support a healthy invertebrate community (Kirby, 1992).

A mature deciduous woodland in Britain typically consists of areas of varying vegetation densities. The proportions of different densities are largely a result of management strategies carried out in the wood. Coppicing, for example, is a common form of woodland management in Britain (Kirby, 1992). Trees are cut at the base and the many branches which subsequently grow from the stump are harvested after a number of years. A coppiced wood has a very dense shrub layer and canopy and, although lacking in large scale variation, the artificial rotation scheme means that there is high biological diversity (Kirby, 1992).

Fully grown coppice, however, may have lower levels of bat activity than more open areas. De Jong (1994) found that few bats were active in dense vegetation in woodland. Aerial insect density in woodlands was been shown by de Jong (1994) to decrease from edges to dense vegetation.

In Britain few researchers have examined bat activity or insect availability in fragmented deciduous woodlands, despite their apparent importance to native chiropteran fauna. In Chapter 4, bat activity in

woodland microhabitats is investigated for uneven distribution. Possible mechanisms causing disproportionate activity in woodlands are examined.

1.5 Diet and prey diversity

Diet analysis has been carried out on a large number of bat species by dissecting faecal pellets and identifying insect fragments (see McAney *et al.*, 1991). Prey types have often been found to be related to the morphology and echolocation calls of the bat species concerned. For example, *M. nattereri* is predicted to be a slow flier with adaptations to slow manoeuvrable flight (Baagöe, 1987). Faecal analysis was carried out by Bauerová and Cerveny (1986) in Czechoslovakia, where the chief components of the diet were Diptera and Coleoptera. Other taxa found in faeces included Arachnoidea, Plecoptera and Orthoptera. Food contained a high proportion of flightless arachnoentomofauna. Also, one of the components was Curculionidae (Coleoptera) which are chiefly diurnal (Bauerová and Cerveny, 1986). This suggests that *M. nattereri* takes a large proportion of its food by gleaning. Similar findings have been made in other diet studies of *M. nattereri* (Shiel, McAney and Fairley, 1991) and for *P. auritus* (Hollyfield, 1993; Poulton, 1929; Shiel *et al.*, 1991; Swift and Racey, 1983).

1.5.1 Pipistrellus pipistrellus diet

Work on *P. pipistrellus* diet has been carried out in Britain by Swift, Racey and Avery (1985) and in Ireland by Sullivan *et al.* (1993) without any separation made between the two phonic types. Of the two phonotypes, the 55kHz type is thought to be the most common in Scotland (Jones, Altringham and Deaton, 1996) where the Swift *et al.* (1985) study was carried out. Both

were conducted close to waterways on faeces collected from bat roosts (Sullivan *et al.*, 1993) and from bats caught in flight in mist nets (Swift *et al.*, 1985). Riverine areas are preferred foraging habitat of the 55kHz type (Vaughan, 1996).

Swift *et al.* (1985) found that the diet of *P. pipistrellus* generally reflected availability of insects. Sullivan *et al.* (1993) found a higher diversity of prey in the faecal pellets of pipistrelles in southern Ireland, however, insect availability was not measured. From Swift *et al.* it could be suggested that foraging by pipistrelles is largely opportunistic and not reliant upon the availability of certain prey types. This hypothesis is investigated in Chapter 5.

Barlow (1997) examined the diet of the two phonotypes and found Psychodidae (Diptera) were the most common prey type in 45kHz faeces, while Chironomidae/Ceratopogonidae (Diptera) were encountered most often in faeces of the 55kHz type. She also found that some 45kHz pipistrelles may glean a small proportion of their prey, because non-flying Chilopoda and Opiliones remains were found in faeces.

In Chapter 5 the diversity and relative abundance of invertebrate taxa are examined in greater detail to determine whether the presence of food types correlate with activity.

Chapter 2

MATERIALS AND METHODS

2.1 Warwickshire

Warwickshire is a gently undulating county with low hills (75m to 130m) and a patchwork of mixed farmland, interspersed with fragmented deciduous woodland often ancient in origin (Tasker, 1991). Towns and villages are scattered throughout. The largest urban area is the City of Coventry which lies to the north west of Warwickshire. Only the most south-westerly region of Coventry lies within modern Warwickshire county boundaries, but for recording purposes Coventry is in the larger vice-county of Warwickshire.

2.2 Woodland sites

Four oak and ash dominated woodlands, varying in size from 4.5 to 78 ha, were chosen as study sites in 1995. One of these, Chase Wood, was used for field work in 1996. Each had been coppiced in areas at some time during their management history. Tocil Wood is a Local Nature Reserve, Roughknowles Wood is managed for timber production, Chase Wood is preserved for hunting, and Long Itchington Wood is a legally protected Site of Special Scientific Interest.

Canopy cover abundance estimates from July 1996 are used in microhabitat descriptions below (see section 4.2.2).

2.2.1 *Tocil Wood* (Figs 2.1a&b): OS Grid Reference SP 303 754

This site covers 4.5 hectares (Fig 2.1a) and is situated on flat ground approximately 75m above sea level (Fig 2.1b). It is a Warwickshire Wildlife Trust Reserve. Records exist for Tocil Wood from 1588 (Warwickshire Wildlife Trust,

Fig 2.1b Tocil Wood transect (thin lines indicate height above sea level)

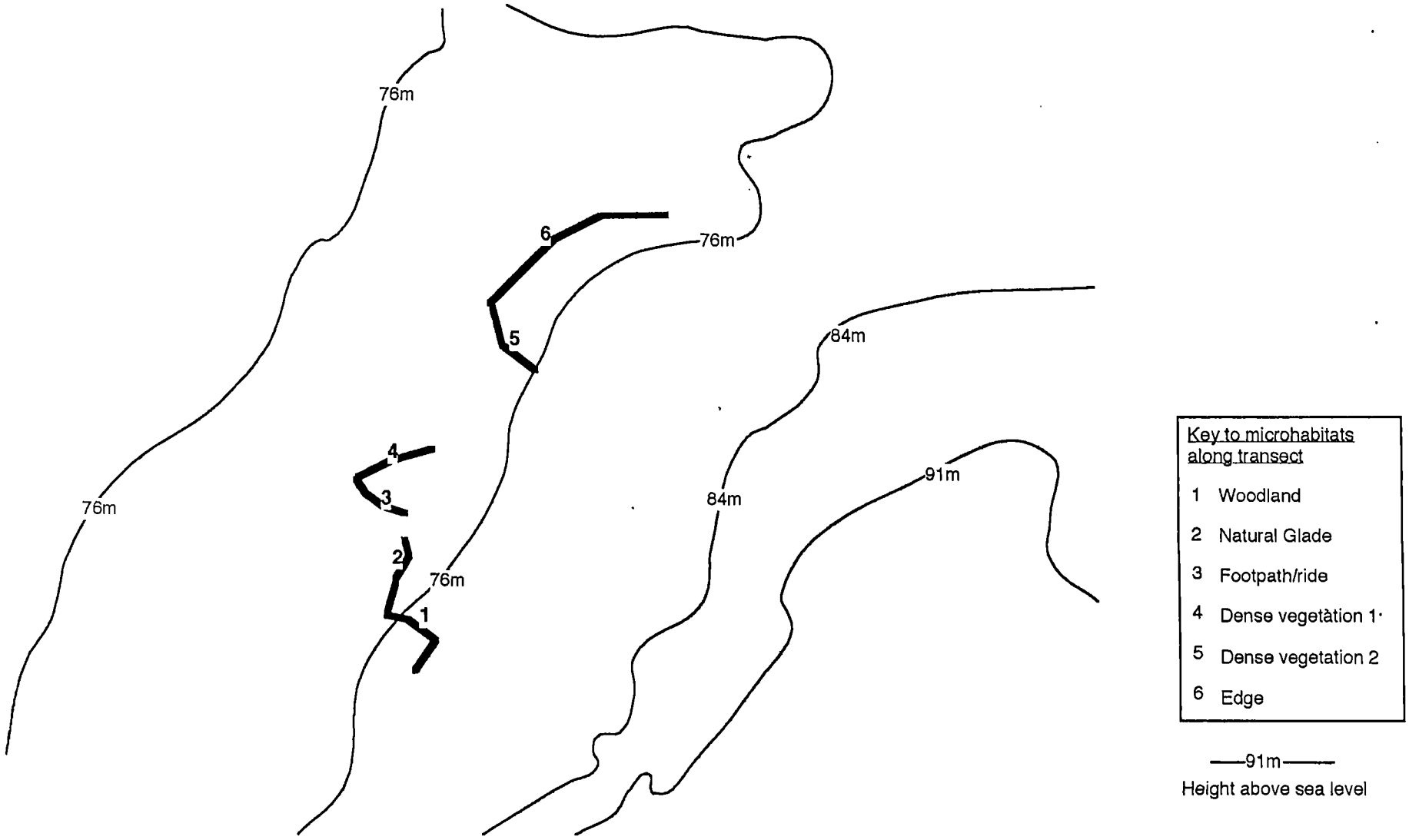


Fig 2.1a Tocil Wood and surrounding landscape

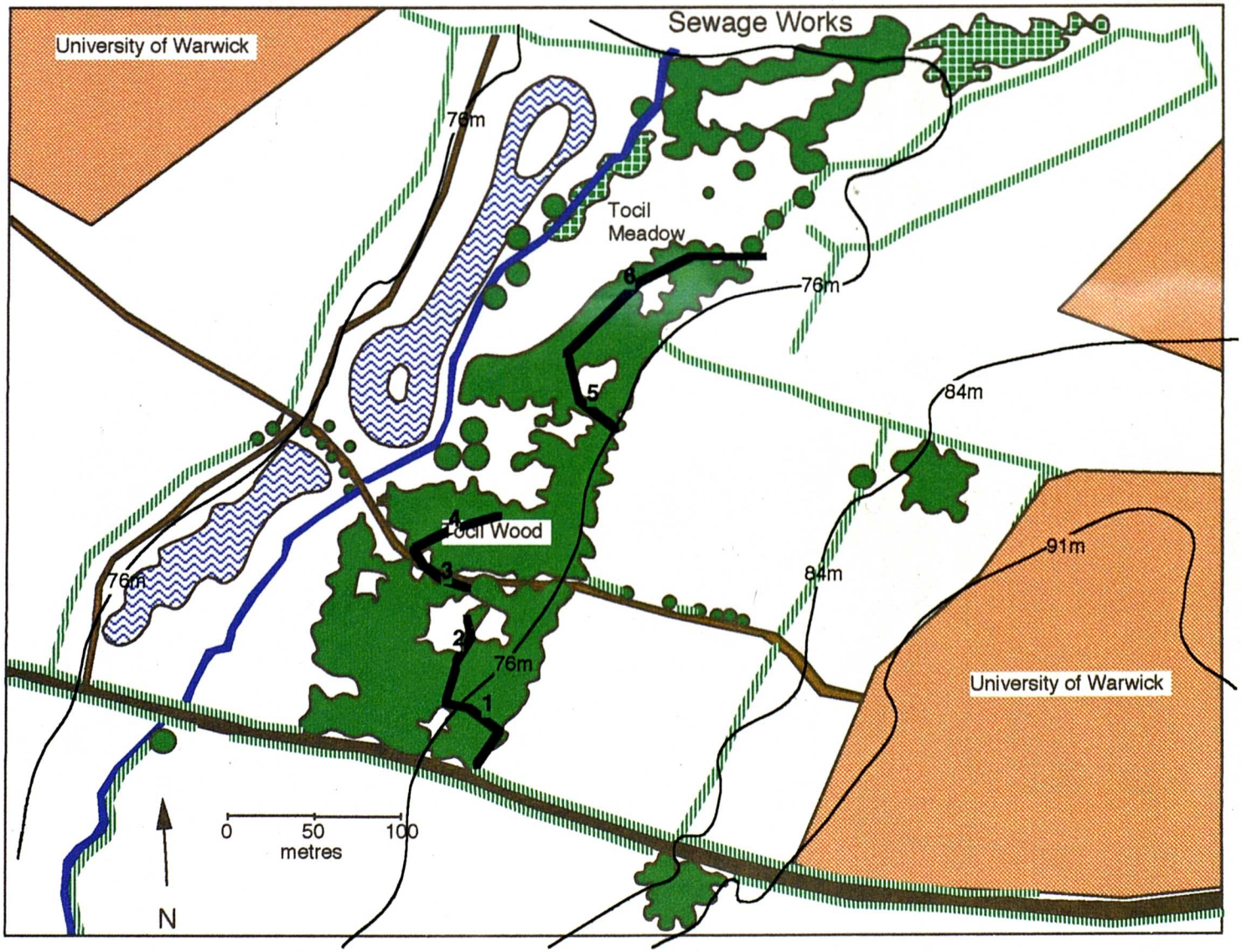
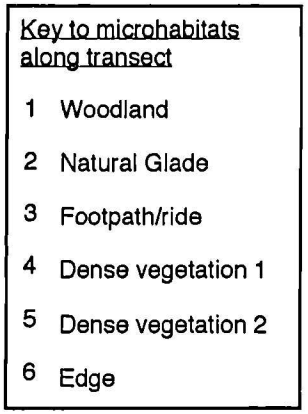
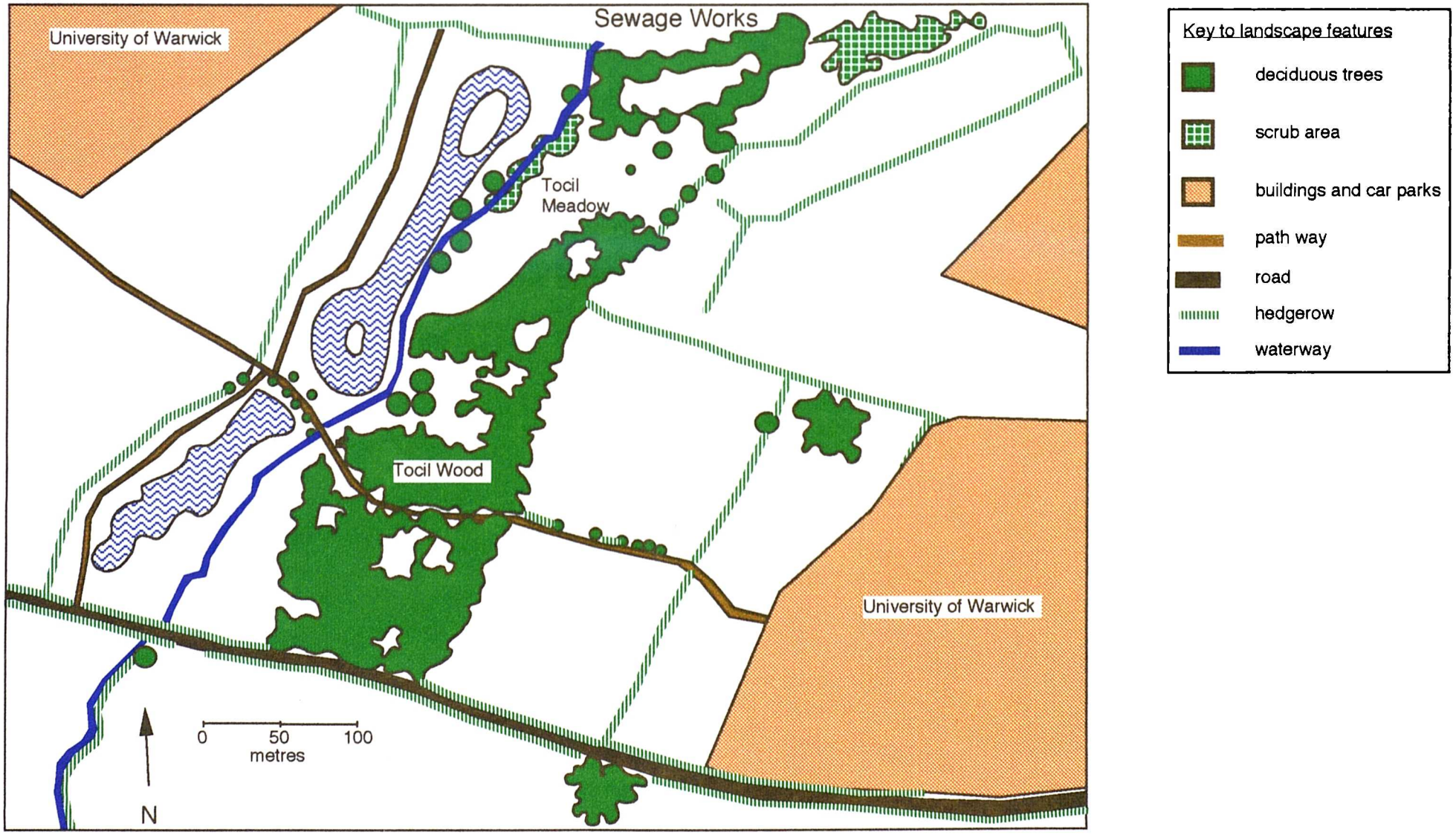


Fig 2.1b Tocil Wood transect (thin lines indicate height above sea level)



—91m—
Height above sea level

Fig 2.1a Tocil Wood and surrounding landscape



1983). Dog's mercury (*Mercurialis perennis*) is considered to be an indicator of ancient woodland (Peterken, 1981) and is present in Tocil Wood.

Tocil is situated on red clay-loams associated with Tile Hill Mudstone, the clay is slightly acidic and slow draining (M. Bradley, pers. comm.). The vegetation in Tocil Wood is dominated by native pedunculate oak (*Q. robur*) and introduced sycamore, there are also some compartments of derelict hazel (*Corylus avellana*) coppice. Persistent sycamore exclusion management is rare in most woodlands (Kirby, 1992).

Tocil Wood is divided into two sections by a footpath which is lined by white (mercury vapour) street lights. There is also a sizeable man-made lake beside the wood which is fed by Canley stream (Fig 2.1a). None of the other woodland sites from this study are in such close proximity to water bodies or artificial lights.

2.2.1.1 Tocil Wood microhabitats

Six microhabitats were covered in Tocil Wood (Fig 2.1b):

1 *Woodland*

Dominated by oak, sycamore and ash standards with an occasional larch (*Larix decidua*), rowan (*Sorbus aucuparia*) and alder (*Alnus glutinosa*), canopy cover averages 46% in this area. There is a shrub layer with some hazel (*Corylus avellana*), holly and elder (*Sambucus nigra*). The field layer is dominated by bracken, bramble, bluebell and sedges (Cyperaceae).

2 *Natural glade*

A break in the sycamore/oak canopy creates a small open glade area. Shrub layer is minimal and the field layer is dominated in late spring by bluebells and in summer by tall and dense bracken.

3 *Footpath/ride*

Herbaceous vegetation borders the cycle track. This is dominated by grass species, nettles (*Urtica dioica*) and docks (*Rumex* spp.). Oak, silver birch (*Betula pendula*) and ash canopy overhangs the track for some of its length. The track is surfaced with tar and is lit nightly with mercury-vapour (white) lights. Herbaceous vegetation bordering the track was mowed once during the summer of 1995 (mid-July).

4 *Dense vegetation 1*

This is an area with sparse hazel coppice and oak/sycamore standards. Canopy cover abundance was estimated at 90%. In the shrub layer there are holly and hawthorn (*Crataegus monogyna*) specimens. The field layer is sparsely vegetated with bramble.

5 *Dense vegetation 2* (Fig 2.2)

This microhabitat consists of derelict and dense hazel coppice with oak and sycamore standards. Estimated canopy cover abundance is 10% but the shrub layer is particularly dense with hazel, holly and rowan. The field layer is patchy and contains bramble.

6 *Edge* (Fig 2.3) **An edge can be described as the border (often linear) formed by a sudden change in vegetation from woodland to field, scrub or road.**

The Tocil edge microhabitat was the border between Tocil Wood and Tocil Meadow. Both are Warwickshire Wildlife Trust Nature Reserves. The edge of the woodland faces north and the meadow is dominated by various grass species, meadowsweet (*Filipendula ulmaria*), and lesser hogweed (*Heracleum sphondylium*). There is some invasion of aspen (*Populus tremula*) and bramble into the meadow. The meadow was mowed in mid-July (1995).

Fig 2.2 Dense vegetation 2, Tocil Wood

Fig 2.3 Edge microhabitat, Tocil Wood

2.2.2 *Roughknowles Wood* (Fig 2.4 a&b): OS Grid Reference SP 287 750

Roughknowles Wood is approximately 7ha in area (Fig 2.4a). It is situated on a north facing slope of Upper Carboniferous Sandstone (British Geological Survey, 1984) and, as a result, the soil is sandy and drains quickly. Elevation of the woodland rises from 84m on its north side to 100m on its south side (Fig 2.4b).

The wood was thinned (conifer trees were removed) in the late 1980's to leave a very open mature woodland of oak trees, mainly *Q. petraea* . The shrub layer is relatively depauperate but there are some relict elder and hazel specimens. The field layer contains a mixture of rosebay willowherb (*Chamaenerion angustifolium*), rushes (*Juncus effusus*), grasses, bracken, bramble and wild raspberry (*Rubus idaeus*). The site has been replanted recently with native trees.

2.2.2.1 Roughknowles Wood microhabitats

Four microhabitats were covered in Roughknowles Wood (Fig 2.4b):

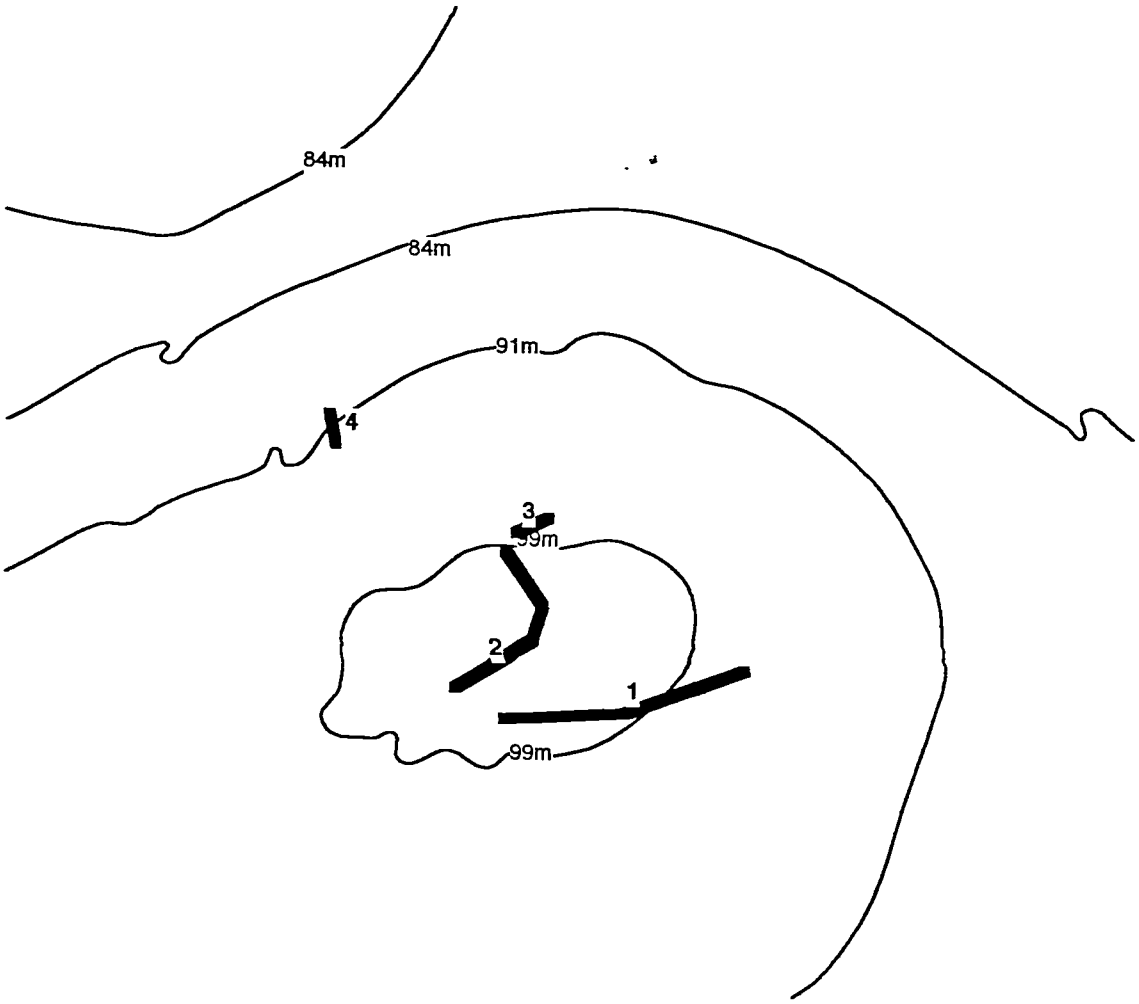
1 *Edge*

The edge microhabitat studied in this woodland is south facing and borders a single track road. It is lined with mature beech trees (*Fagus sylvatica*). There is no vegetation between the road and woodland edge.

2 *Open woodland 1* (Fig 2.5)

This section of the transect follows an old track through the centre of the woodland. Canopy cover abundance (oak) averages 2.5%. Very low densities of hazel consitute the insubstantial shrub layer. The herbaceous field layer consists of a mixture of rushes, sedges, grasses, bramble and willowherb, low densities of bracken and some wild raspberry.

Fig 2.4b Roughknowles Wood transect (thin lines indicate height above sea level)



Key to microhabitats along transect

1 Edge

2 Open Woodland 1

3 Open Woodland 2

4 Dense vegetation

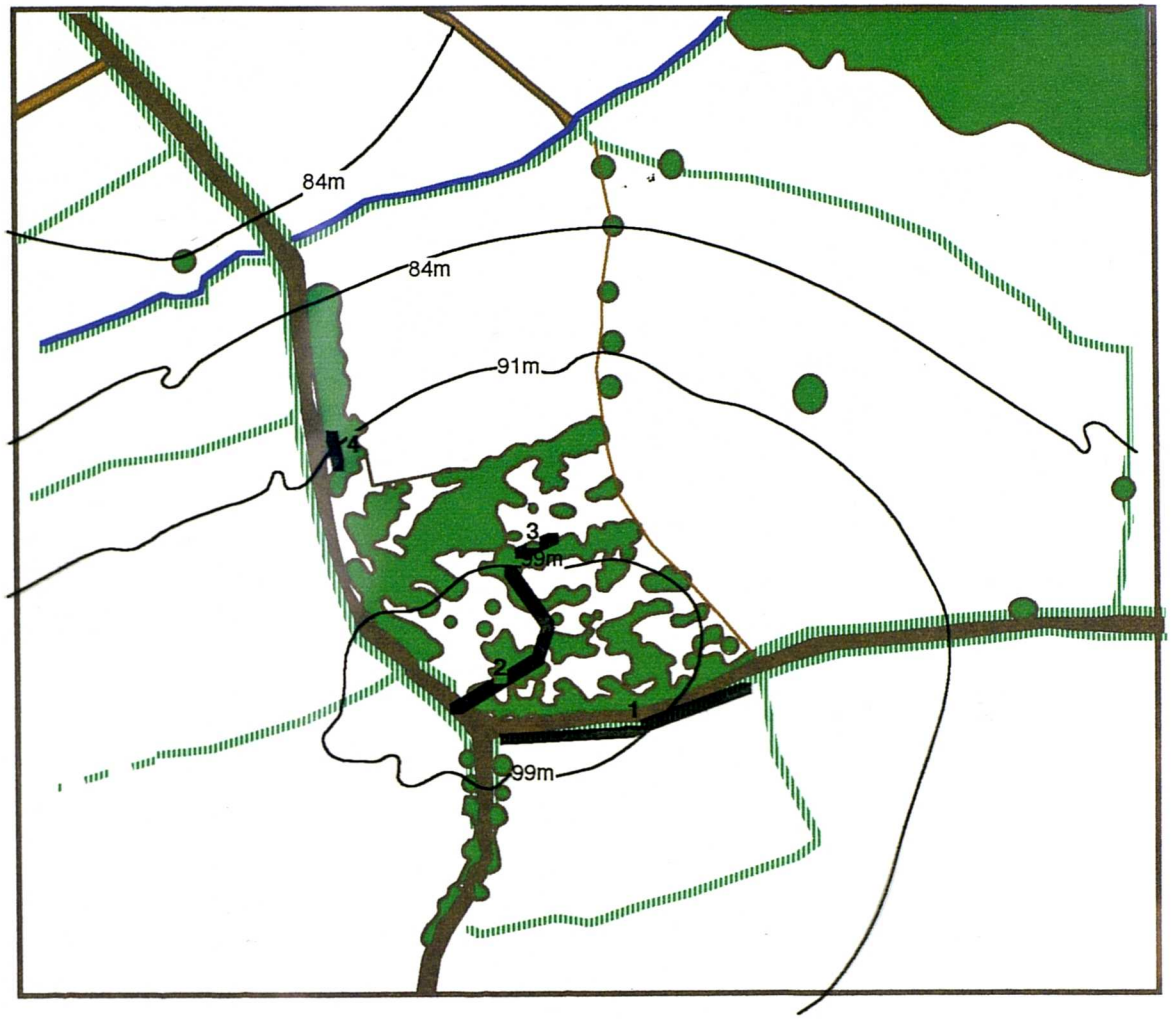
99m

Height above sea level

N

Fig2.4a Roughknowles Wood and surrounding landscape

Fig 2.4b Roughknowles Wood transect (thin lines indicate height above sea level)



Key to microhabitats along transect

1 Edge

2 Open Woodland 1

3 Open Woodland 2

4 Dense vegetation

99m

Height above sea level

Key to landscape features

deciduous trees

path way

road

hedgerow

waterway

fence line

0 100 200
metres

N

Fig2.4a Roughknowles Wood and surrounding landscape

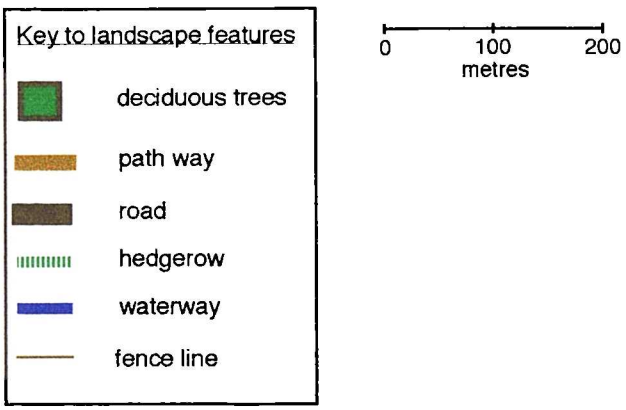


Fig 2.5 Open woodland 1, Roughknowles Wood

3 *Open woodland 2*

In this microhabitat the field layer is dominated by willowherb, while raspberry, grasses, foxglove (*Digitalis purpurea*) and bramble are also present. Canopy cover by the mature oak trees is estimated at 0.5%.

4 *Dense vegetation*

Canopy cover abundance is estimated at 45%, 15% of this is beech while the remainder is oak. There is a dense shrub layer consisting of old hazel

coppice, young beech and oak trees. The field layer consists of bramble and some grass.

2.2.3 *Chase Wood* (Fig 2.6 a&b): OS Grid Reference 257 727

Chase Wood is a 25 ha woodland situated on a south facing slope (Fig 2.6a). The woodland rises in elevation from 91m to 114m (Fig 2.6b). The woodland is mixed with a small conifer plantation on the west side. This plantation site was not included in this study. The woodland is used as a hunting resource.

The canopy consists mainly of mature oak (*Q. robur*) with some ash. In the lower (southern) half of the wood, silver birch is a major canopy former. Bluebells flower throughout the wood in late spring.

Chase Wood lies on the Triassic Mercia Mudstone group and underlying clays are heavy and poorly draining (British Geological Survey, 1984).

2.2.3.1 Chase Wood microhabitats

Six microhabitats were studied in Chase Wood (Fig 2.6b):

1 *Natural glade* (Fig 2.7)

Canopy cover abundance in this natural clearing averages 23%, and consists mainly of oak trees. The field layer is composed of dense bluebell and bracken cover.

2 *Woodland*

This microhabitat has an average canopy cover abundance of nearly 50%. The majority of the canopy forming trees are oak with interspersed ash. There is little shrub layer and the field layer consists mainly of grasses with scattered bramble, pendulous sedge and *Vicia* spp (vetches). The herbaceous layer was mown in mid-July 1995.

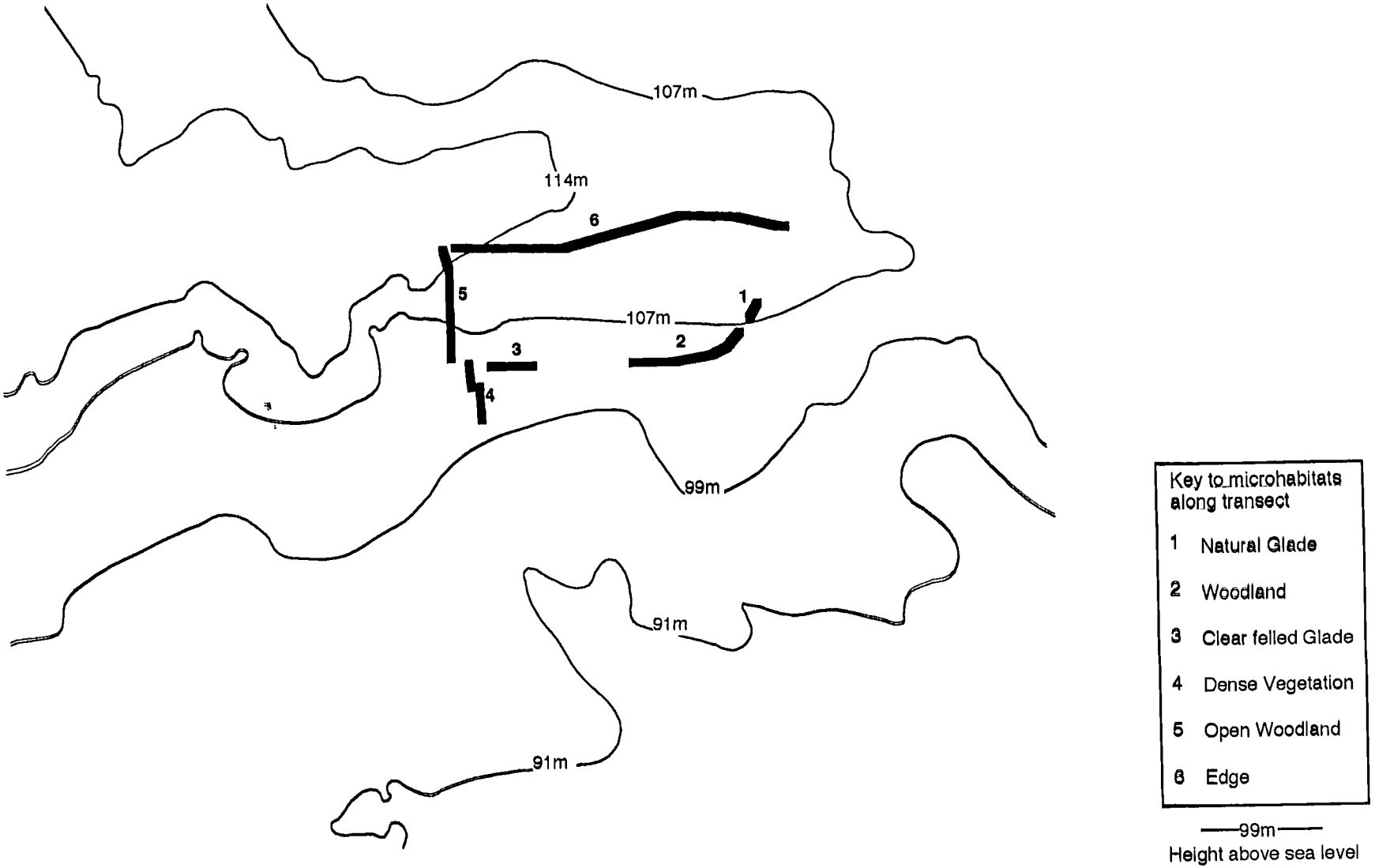
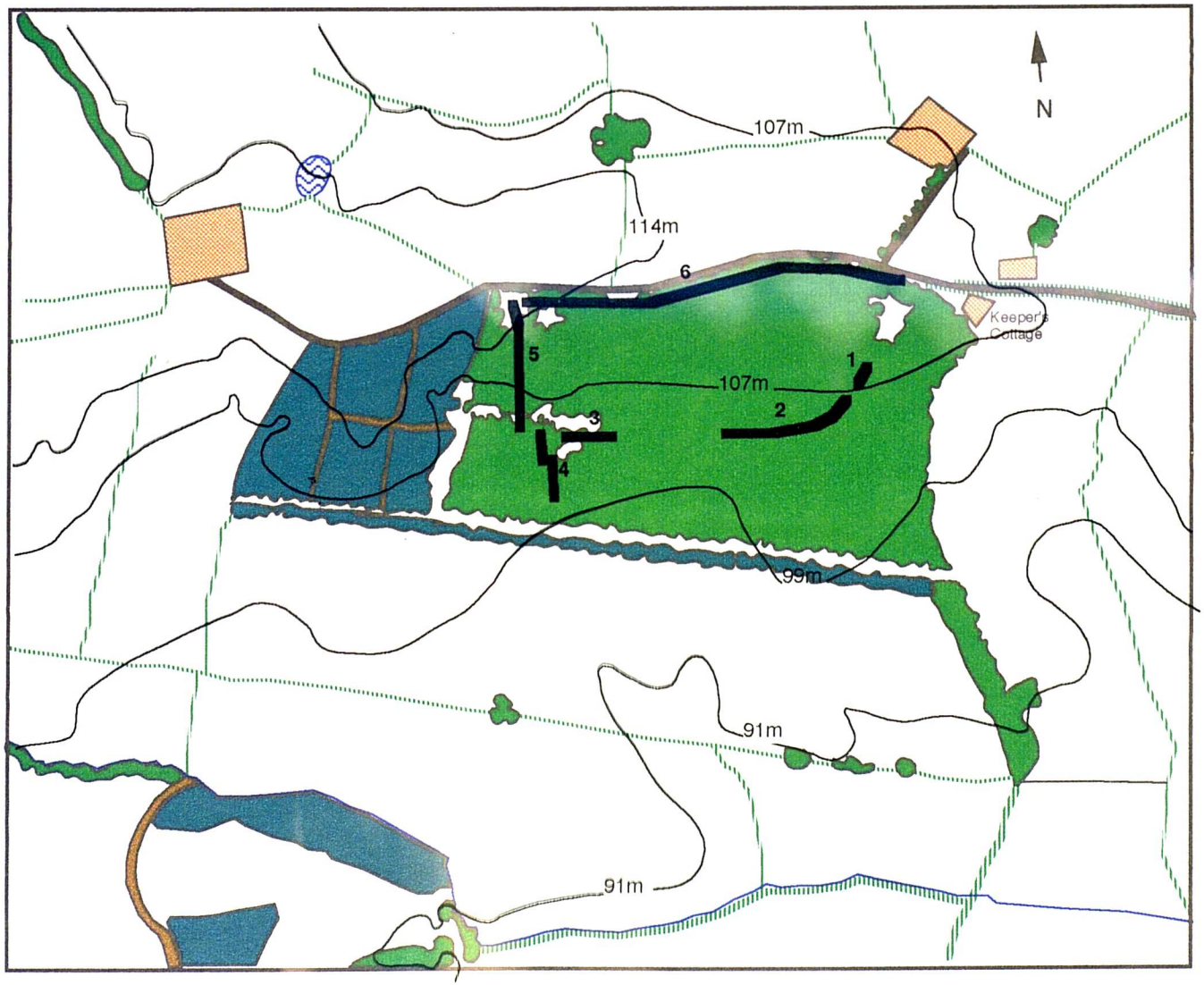
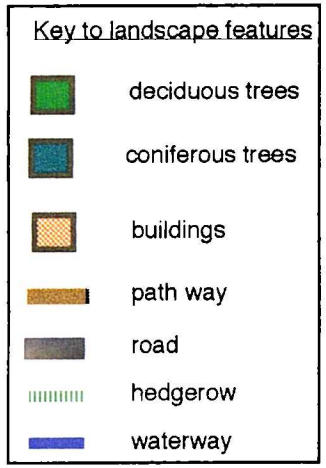
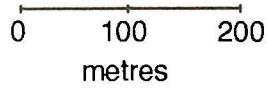


Fig 2.6b Chase Wood transect (thin lines indicate height above sea level)







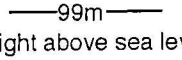


Fig 2.6a Chase Wood nd surrou ndscape

Fig 2.6b Chase Wood transect (thin lines indicate height above sea level)

Fig 2.6a Chase Wood and surrounding landscape

Fig 2.7 Natural glade, Chase Wood

3 *Clear-cut*

This rectangular area of approximately 50x30m has a grassy field layer with some docks and nettles. The herbaceous vegetation was cut in mid-July 1995. The area is used as a run for pheasant hunting.

4 *Dense vegetation*

Average canopy cover abundance here is 67%: 14% of which is formed by oak and silver birch the remainder. The shrub layer is particularly dense

with holly and hazel bushes. The field layer is sparse but bramble and ferns occur intermittently.

5 *Open woodland*

Cover abundance of the canopy in this area is approximately 40%. Most of this is oak with some silver birch. The shrub layer is sparse with a few hazel specimens. Grass and bramble make up the field layer.

6 *Edge*

The woodland edge microhabitat borders a single track road. There is a small grassy verge between the woodland and the road.

2.2.4 Long Itchington Wood (Fig 2.8 a&b): OS Grid Reference 38 62

Long Itchington Wood (also known as Ufton Wood) is a privately owned and managed Site of Special Scientific Interest. It is maintained as a timber resource: relatively large areas are felled and replanted on rotation. The wood is also coppiced on rotation.

The woodland is 78ha (Fig 2.8) and ranges in altitude from approximately 85 to 110m (Fig 2.8b). Most of the woodland is situated at 105m,. However, on the north side of the woodland White Lias (white limestone) bedrock borders with softer mud stones (British Geological Survey, 1984) resulting in a steep drop in height to 85m.

The canopy is dominated by *Q. robur* with some ash and occasional *Q. petraea*. This woodland has been described as one of the best remaining examples of coppice-with-standards woodlands that is still managed traditionally in the English midlands (WBRC). The shrub layer is species rich but is dominated by hazel and some field maple (*Acer campestre*).

Fig 2.8b Long Itchington Wood transect (thin lines indicate height above sea level)

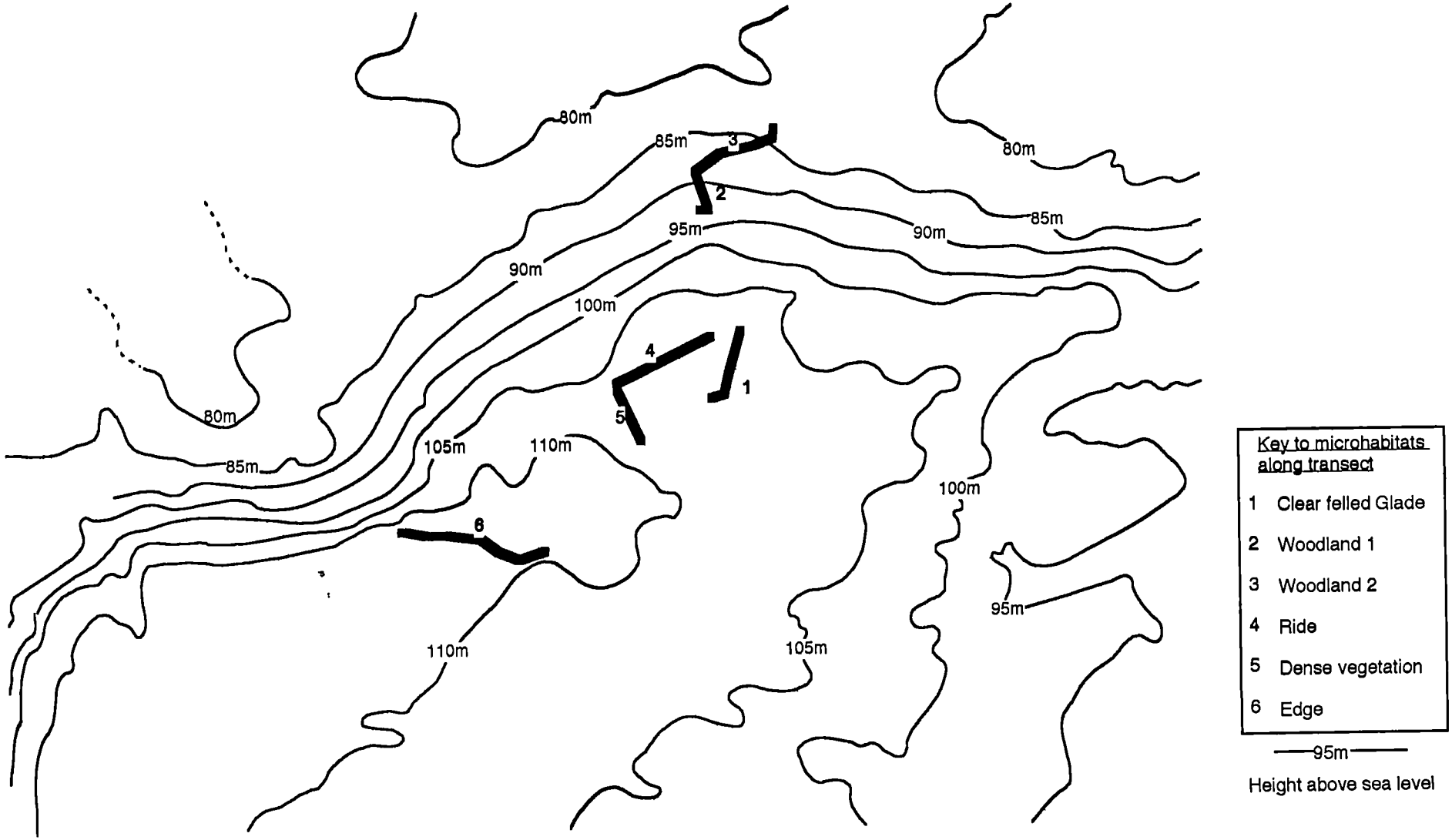


Fig 2.8a Long Itchington Wood and surrounding landscape

Fig 2.8b Long Itchington Wood transect (thin lines indicate height above sea level)

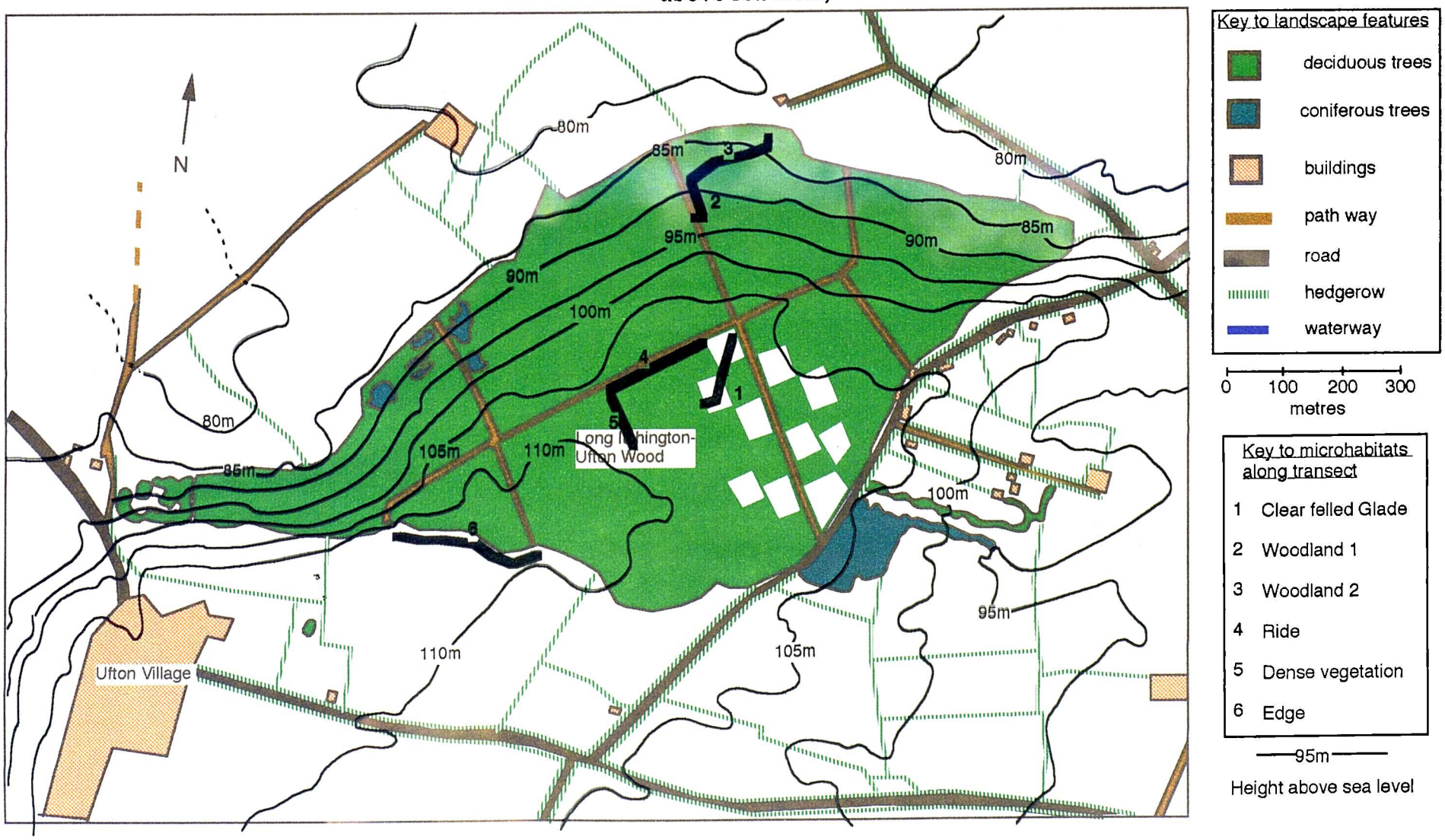
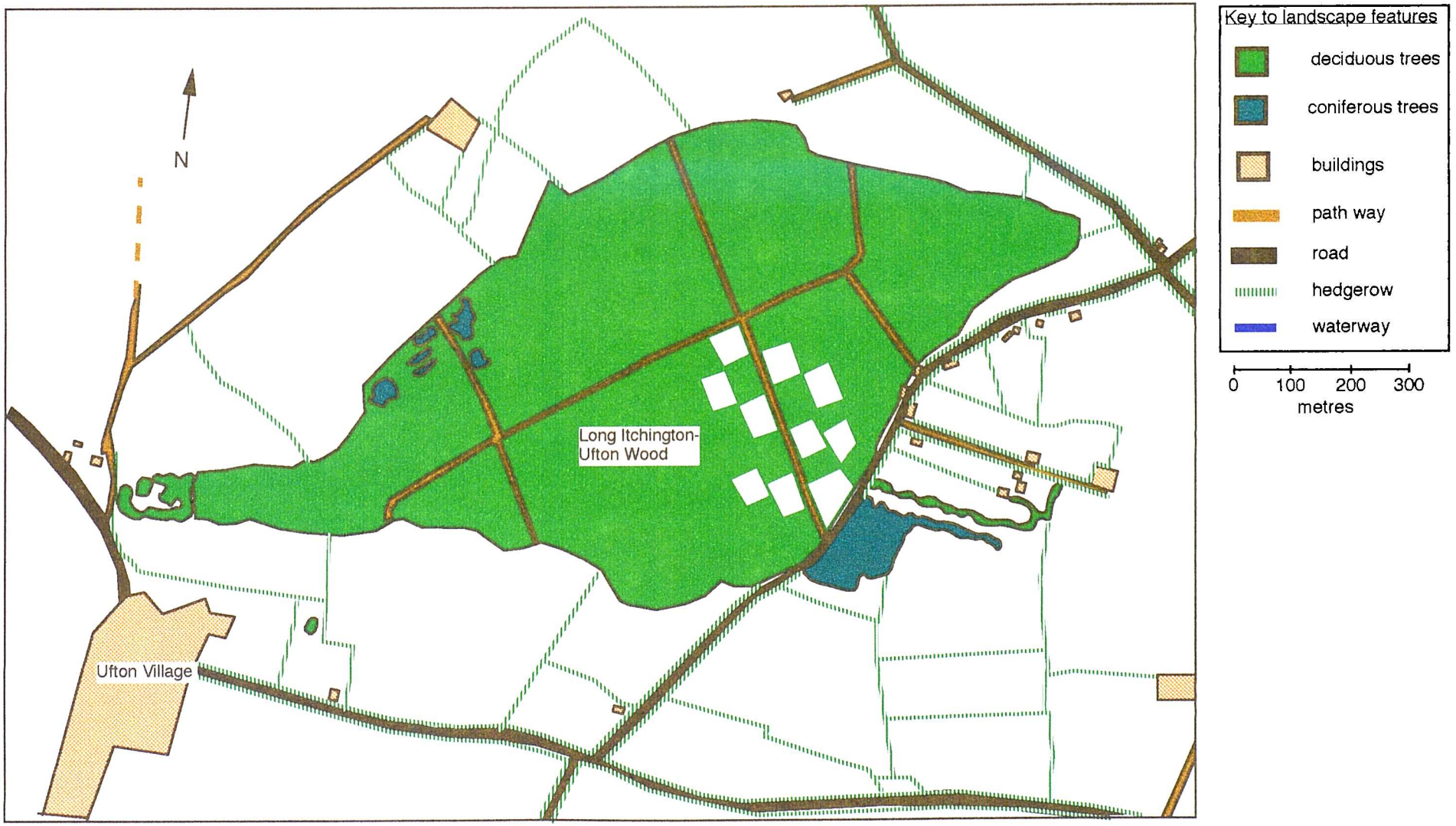


Fig 2.8a Long Itchington Wood and surrounding landscape



2.2.4.1 Long Itchington Wood microhabitats

Six microhabitats were studied in Long Itchington Wood (Fig 2.8b):

1 *Clear-cut* (Fig 2.9)

Extensive clear felling took place in the early 1990's of several large 200x200m areas within the woodland (white areas in wood in Fig 2.8a). One of these was studied as a clear felled glade. The area has been replanted. Borders with mature trees are linear and field layer vegetation consists of tall grass species with some pendulous sedge (*Carex pendula*) and thistles (*Cirsium* spp.).

Fig 2.9 Clear-cut, Long Itchington Wood

2 *Woodland 1*

This microhabitat is situated on the north facing slope of the wood. The canopy is dominated by mature oak trees (cover abundance approx. 70%).

The shrub layer consists of hawthorn, hazel and young ash. The field layer is made up of scattered bramble, grass, bracken, pendulous sedge and burdock (*Arctium minus*). The 100m of Woodland 1 covers a steep descent.

3 *Woodland 2*

Canopy here is dominated by oak trees (approximately 75% cover abundance). The shrub layer is less dense than in Woodland 1, with a mix of hazel, young ash and hawthorn. Bramble is the main field layer species. This microhabitat is situated at the foot of the north facing slope on fairly level ground.

4 *Ride* (Fig 2.10)

This long straight ride microhabitat consists of a pathway (2-3m wide) covered in grasses, pendulous sedge, briars and wild roses (*Rosa canina* and *R. arvensis*). Some of the woodland shrubs have spilled over onto the track, e.g. blackthorn (*Prunus spinosa*) and hazel. Little of the ride is covered by canopy (estimated canopy cover abundance 4%).

5 *Dense vegetation* (Fig 2.11)

Average canopy cover abundance here is 96%. Ash and oak dominate and mature field maples are also present. This part of the transect was covered by walking along an old ditch, on one side felling had taken place in 1923 (WBRC) and the relatively young ash trees form a particularly dense canopy. On the other side trees are more mature although canopy was also dense. The shrub layer along this section is composed of hazel, ash and maple. The field layer is patchy with some grasses and sedges.

Fig 2.10 Ride, Long Itchington Wood

Fig 2.11 Dense vegetation, Long Itchington Wood

6 *Edge*

The edge microhabitat is south-west facing. The woodland border runs along arable land which was used to grow a wheat crop during 1995. There is a narrow stretch of grass turf (1-2m) between the field and woodland.

2.3 Bat activity

2.3.1 Bat detector

A Stag Electronics, Bat Box III tuneable heterodyne bat detector was used throughout this project. It is powered by one 9V battery.

2.3.2 Bat activity

Bat activity was estimated using a method based on Ahlén (1981) and de Jong (1994). A line transect was mapped out in each wood. Transects covered known lengths of different microhabitats within woods: natural glades, rides, clear-cuts, dense vegetation (such as coppice or closely growing saplings), naturally open canopy and woodland edges.

A transect was covered at normal walking speed between three and nine times during the night. The first survey was started half an hour after sunset and the last was completed half an hour before dawn. The number of transects covered depended upon transect length and hours of darkness.

Transect survey start time and number of bat passes were recorded. Bat Box III was used to observe bat passes. From the time an echolocating bat came into range of the bat detector until it left was recorded as one bat pass. Normally, the highest number of echolocating bats distinguishable simultaneously was two.

However, this meant that only two bats could be detected whenever high densities of bats were present for an appreciable length of time. This situation was uncommon but it did arise on several occasions.

A different approach to measuring bat passes was necessary. Instead, the loudest echolocation sequence was followed aurally until the sound was replaced by a more intense call. One such sequence was taken as a single bat pass. This method may be less accurate than measuring activity when few bats are present, however, it prevented an excessive underestimation of activity due to continuous streams of echolocation calls.

The detector was tuned to 45kHz except when attempting to identify species. It was possible to discriminate between the two phonotypes of *P. pipistrellus*. This was done from July 1995 onwards. It was also possible to discriminate between *P. pipistrellus* and *Myotis* species. However, *Myotis* spp. were virtually indistinguishable unless the distance between the observer and flying bat and the bat's flight style characteristics were apparent. Other species of bat were rarely detected.

Field work was carried out from late March until mid-September, 1995. Twelve nights were spent in Chase Wood, and 13 nights in each of the other woodlands. No field work was carried out in Chase Wood in late March. In Roughknowles, field work was abandoned after the first transect on 23/4 due to poor weather conditions.

For correlation and regression analyses, bat activity was calculated as the average number of bat passes per 100m of transect (or microhabitat) for each night.

In 1996, activity was monitored in Chase Wood from late May to late July 1996 (11 nights). Observations began when bats were known to have emerged

from the adjacent 45kHz phonotype *P. pipistrellus* roost. Five minutes were spent in each microhabitat observing echolocating bats in flight (from a fixed observation point) using a detector and strong torchlight. Torchlight was provided by Clulite torches (Cluson Engineering). An index of bat activity per unit time was calculated for each microhabitat (no. of passes per 5 minutes).

2.4 Insect abundance

2.4.1 Insect sampling methods

Insects were sampled simultaneously with bat activity monitoring. A suction and a light trap were set up in a glade within the study woodland and sweep net samples were taken in each microhabitat after it had been covered on a transect walk.

2.4.1.1 Suction trap (Fig 2.12)

A Johnson-Taylor insect suction trap was set up in an open area of each wood and run from a portable Kawasaki generator. The trap has a 23cm Vent Axia fan and the opening was positioned 3m from the ground. Insects are separated on an hourly basis by descending discs covered in permethrin soaked cotton fabric. The suction trap was started at sun down and left running until dawn.

Trap efficiency can be affected by varying wind speeds and insect size (it is biased towards small aphid sized insects) (Taylor, 1962). However, this trap was placed in relatively sheltered glades during the study and wind never reached high speeds. Log correction factors can be applied to the numbers of

insects caught to obtain an absolute density of aerial insects present (Service, 1993). However, relative abundance was considered sufficient in this case.

In the laboratory, the catch was sorted into containers, labelled and frozen for identification.

Fig 2.12 Suction trap (in Chase Wood, April 1995)

2.4.1.2 Ultraviolet Light Trap

A UV light trap was set up in an open area approximately 10m from the suction trap. This trap catches insects attracted to the UV part of the

electromagnetic spectrum. Insects fall into a funnel and are deposited inside the box. The bottom of the trap is lined with egg-boxes to provide resting places. UV light traps particularly attract Lepidoptera (noctuids) (Southwood 1978) and are generally biased towards larger insects than the suction trap (Hollyfield, 1993).

The trap was run from dusk until dawn and powered with a car battery. The entire box and its contents were removed to the laboratory where they were placed in the freezer for approximately 10-20 minutes. This facilitated easy removal of the contents. The catch was placed in containers, labelled and frozen.

2.4.1.3 Sweep Netting

Sweep net samples of invertebrates were taken in each microhabitat along each transect. Six 180° sweeps were taken from a stationary position, the first two across the top of understorey vegetation (which served to disturb resting invertebrates), the second two approximately one metre above understorey vegetation and the final two in a vertical arc above the sweeper. The sweep net pole measured 3m.

Insect catches were bottled with a small piece of paper tissue soaked in a 1% permethrin insecticide solution. Catch samples were labelled and stored in a freezer.

The number of insects caught in each microhabitat was calculated. Results were corrected to $1000m^3$ using Tonkyn's (1980) equation for the volume sampled by the sweep net.

The volume sampled by a net in a 180° arc from a stationary position is:

$$B(\pi r)$$

Where:

B = area of opening of the net

r = length of sweep net handle

2.5 Lunar Cycle

To remove possible bias caused by lunar effects on bat or insect behaviour, field work was carried out on the same four nights of each lunar cycle in 1995. The woodlands were studied consecutively on four nights around the new moon and mid-way between the new and full moon from late March to September 1995 (Chase Wood was studied from early April). The sequence in which woodlands were studied was chosen randomly.

In 1996 field work was carried out irrespective of stage of the lunar cycle.

2.6 Computing

Data were initially entered into Excel 3.0 (for Macintosh) for sorting and statistical analyses were carried out using SYSTAT 5.2.1. A program for Chi-square analysis was kindly provided by the Computing Services Dept., University of Warwick. Graphics were completed using SYSTAT or Excel followed by Mac Draw Pro 1.5v2.

Chapter 3

LOCATING BAT ROOSTS USING A QUESTIONNAIRE SURVEY AND *PIPISTRELLUS PIPISTRELLUS* RINGING AND ROOST COUNTS

3.1 Introduction

3.1.1 Estimating bat and bat roost densities

Various techniques have been employed to produce estimates of roost density and bat activity in different habitats by using bat detectors (e.g. de Jong and Ahlén, 1991; de Jong, 1994; Rydell *et al.*, 1994). The British Bats and Habitats Survey provided information on usage of different habitats throughout Britain using bat detectors (Walsh *et al.*, 1995; Walsh and Harris, 1996 a&b).

Kronwitter (1988) carried out a census of *N. noctula* by surveying bat boxes and radio tagging any individuals found there. By following bats as they moved, Kronwitter located a network of roosts, estimated the spread of the population and then calculated its density.

Wiles, Lemke and Payne (1989), estimated population densities of fruit bats on the Mariana Islands based on the number of bats recorded leaving the roosts, the size of the island, amount of forest cover and food plant diversity.

Speakman *et al.* (1991) determined roost densities following an intensive poster campaign around the Rivers Dee and Don in Scotland. They then estimated roost numbers, mean roost size and subsequently a minimum population density of *P. pipistrellus* at 18.2km^{-2}. Jones *et al.* (1996), using a similar method, estimated minimum population densities of *P. pipistrellus* in Northern England to be lower at 12.6 bats.km^{-2}.

3.1.2 Questionnaires

Questionnaires have occasionally been used as methods of determining wild animal abundances. Abe *et al.* (1991), in their survey of the introduced mongoose on Japanese Islands, used questionnaires as well as trapping and direct observations to estimate population sizes.

The decline of the black grouse population in Northern England has been documented from bag records and this has been confirmed by questionnaire surveys (Baines and Hudson, 1995).

In North America the Federal Waterfowl Hunter Questionnaire Survey is used to estimate harvests of waterfowl as well as hunter activity. However, it has been noted that non-responses lead to bias in estimates of proportion of active hunters and produce overestimates of both harvests and hunting activity (Pendleton, 1992). This underlines one of the difficulties with questionnaire surveys, upon analysing results: deciding how to approach the unreturned questionnaires.

Mail questionnaires can only be used with literate respondents who are assumed to be highly motivated about the topic being studied (Bourque and Fielder, 1995). Among the advantages to mail surveying are its low cost (compared with telephone interviews) and the fact that it reaches people who may be reluctant to talk to strangers. The main disadvantage to mail questionnaires is their low response rate. It is estimated that in a single mailing incorporating no incentives the surveyor can expect a 20% response rate (Bourque and Fielder, 1995). Fowler (1984) suggested that a return rate of less than 30% could be expected.

In order to achieve a good response rate the questionnaire must be carefully designed (Fowler, 1984; Dillman, Sinclair and Clark, 1993). Features which make a mail questionnaire more attractive have a positive effect on response rates. Also response tasks should be as simple as possible e.g. tick boxes (Fowler, 1984).

In Britain, membership of environmental and conservation related organisations is generally very high. The nature conservation movement as a whole has an estimated combined membership of more than 4 million people (Evans, 1992). This high level of interest in wildlife issues renders it is likely that a wildlife survey would be favourably received by the general public.

3.1.3 Suitability of survey areas to bats

Land use in Warwickshire has been briefly described in Chapter 2 (section 2.1). With many scattered deciduous woodlands, a network of hedgerows and some waterways it is likely to support reasonable bat populations. Limpens and Kapteyn (1991) working in the Netherlands, observed that small bat species would not cross open habitats but only follow linear landscape features when travelling from one area to another (see also section 1.4.1.1). A lack of hedgerows or linear landscape features is unlikely to be a factor limiting population sizes in the survey areas.

Of the eleven species which have been recorded in Warwickshire to date, there are several which are unlikely to be found using a questionnaire survey to householders, either because they are rare (e.g. *R. hipposideros*, *N. leisleri*, and *E. serotinus*) or because their roosting habits render them less obvious than other species (e.g. *N. noctula* which roosts in trees (Corbet and Harris, 1991; Kronwitter, 1988)). The following species are those which are most likely to be located using a questionnaire survey in Warwickshire.

P. auritus often gleans insects from vegetation (Cranbrook, 1963) and is known as an almost exclusively woodland foraging bat (Corbet and Harris, 1991; Entwistle *et al.*, 1996). There are many deciduous woodlands scattered throughout the questionnaire survey sectors providing potential foraging areas. Potential roost sites for this species are also plentiful as many of the houses, barns and churches are in excess of two and three hundred years of age. *P. auritus* are commonly found in attics of old houses with large roof spaces (e.g. Entwistle, Racey and Speakman, 1997) and often use feeding perches in porches or outbuildings (Corbet and Harris, 1991; Stebbings, 1993). *P. auritus* is the second most frequently recorded bat in Warwickshire, after *P. pipistrellus*. Jones *et al.* (1996) have noted a geographic trend in *P. auritus* populations: abundance declines as human population density increases.

Modern houses are also abundant in the survey areas. Pipistrelle nursery roosts are commonly found in modern houses (Corbet and Harris, 1991). Pipistrelles use a wider range of foraging areas than brown long-eared bats. They are known to forage in riparian areas and around woodland edges and streetlights (Corbet and Harris, 1991; Rydell, 1992). Jones *et al.* (1996) noted an increase in the density of pipistrelle roosts towards human population centres.

Myotis spp. have been observed foraging in woodlands in the survey areas (see section 4.3.1), although records for *Myotis* spp. are scarcer than for the long-eared or pipistrelle species (WBRC).

Occurrences of *M. daubentonii* bats in survey areas are likely to be limited by a lack of waterways. As well as feeding mainly over the water surface (Swift and Racey, 1983), *M. daubentonii* often roosts close to water (Speakman *et al.*, 1991; Corbet and Harris, 1991).

Whiskered/ Brandt's (*M. mystacinus /brandtii*) may be more frequently recorded from the survey than Daubenton's because they are often observed in wooded country. *M. brandtii* generally has a preference for larger wooded areas than its sibling species, *M. mystacinus* (Gaisler, Vlasín and Bauerová, 1989; Taake, 1984).

From the autumn of 1993 to the summer of 1994 attempts were made to locate roosts in the area by inspecting buildings whose map location and status suggested that they were likely to contain a roost appealing for information through the local radio stations and newspapers

These techniques led to the identification of five roost sites in the area (see Fig 3.2). It was considered unlikely that this represented more than a small fraction of roost sites in the area.

3.1.4 Roost counts

Roost counts have been conducted by many researchers and bat groups, both automatically (using infra-red bat counters) and manually (e.g. Catto *et al.*, 1995; Jones *et al.*, 1996; Maier, 1992; Racey *et al.*, 1987; Swift, 1980). Counts have been carried out for many reasons, for example, to determine activity during the night, population levels and dates of emergence of young.

Roost counts were carried out at Keeper's Cottage (see Fig 2.6a) to determine the size of the population associated with the roost. It was possible that individuals normally associated with the roost were not emerging, emerging via a different exit (e.g. along part of the roof which was not visible) or were not present on the night of counting. For these reasons an estimate was made of the size of the colony previous to young becoming volant using the numbers of marked individuals noted emerging.

3.1.5 Emergence times

Jones and Rydell (1994) hypothesised that emergence times of different bat species may largely be a function of their dependence on the dusk peak of in aerial insect availability along with their ability to avoid predation by diurnal birds. Hence, gleaning bats and those that feed extensively on moths were predicted to emerge later than aerial-hawking species that feed on small flying insects.

Jones and Rydell compiled information from many studies world-wide and found that emergence times were significantly correlated to proportion of flightless taxa in the diet and wing loading (manoeuvrability). The mean emergence time calculated for bats that feed mainly on aerial prey was 27.2min after sunset. However, the Keeper's Cottage roost is situated directly beside a woodland and it is possible that bats there will emerge earlier there because bats can immediately avail of shelter from the woodland canopy.

3.2 Materials and methods

3.2.1 Study areas (see Figs 3.1&3.2)

The survey was conducted within specified areas. Three areas (A, B & C) were situated side by side to the south west of Coventry (Fig 3.1). These totalled 25km^2 in area. A fourth survey area was situated around Long Itchington/Ufton Wood (D) further south (Fig 3.1). Despite features in the survey areas which could be considered favourable to bats, such as woodlands and hedgerows, prior to 1993 very few roosts or even flying bats had been recorded in these areas.

Study areas were chosen to include land surrounding Long Itchington, Chase, Roughknowles and Tocil Woods. Urban areas were mainly avoided, although, in areas C and A, the outskirts of Coventry and Kenilworth were included.

- **Area A** (8km^2) is situated in the south westerly tip of Coventry City. This area includes the University of Warwick Campus, Tocil Wood Nature Reserve and Wetlands and several new housing developments in close proximity to mature deciduous woodland. Roughknowles Wood is also situated within A. The highest density of buildings is located in the east, mainly suburban dwelling houses. The area is not heavily industrialised but roads become quite congested with commuter traffic. The west is mainly agricultural land with fragmented woodlands. Street lights line most roads. These are known to attract some species of foraging bats (e.g. Fenton *et al.* 1983; Hickey and Fenton, 1990; Rydell, 1992; Blake *et al.*, 1994). However, the street lights present are mainly orange. High densities of bats are usually only noted around mercury-vapour street lamps which emit white light, as opposed to roads lit with orange (sodium bulbs) or unlit roads (Rydell and Racey, 1995). Of the four areas, A is likely to be

most polluted and perhaps more disturbing to bats (high noise levels) than others.

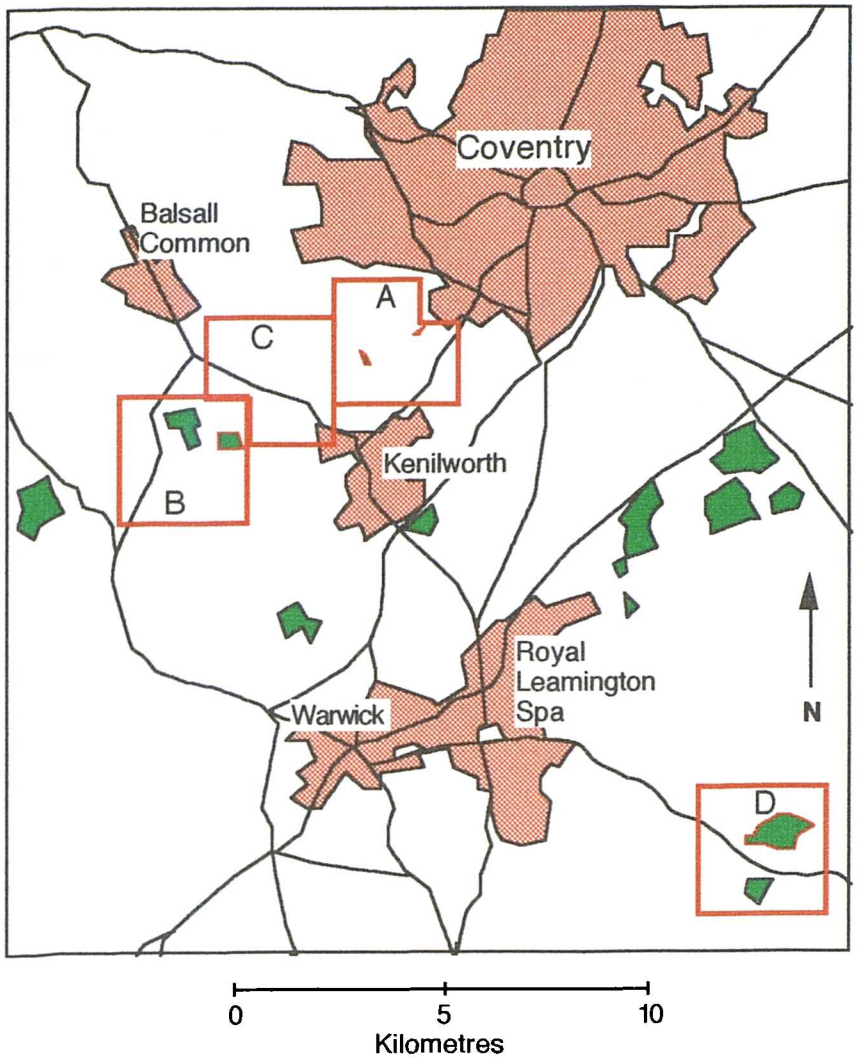


Fig 3.1 Questionnaire survey areas and surrounding towns and cities. Major roads in black. Woodlands used for field work outlined in red.

- **Area B** (9km^2) is mainly agricultural land with associated farmhouses and out buildings. Haseley Knob, a small village with both old and modern houses is situated to the south. Land is flat with many small woodlands two of which are relatively large and one covers an area of approximately 1km^2. There are some small ponds but no substantial waterways.

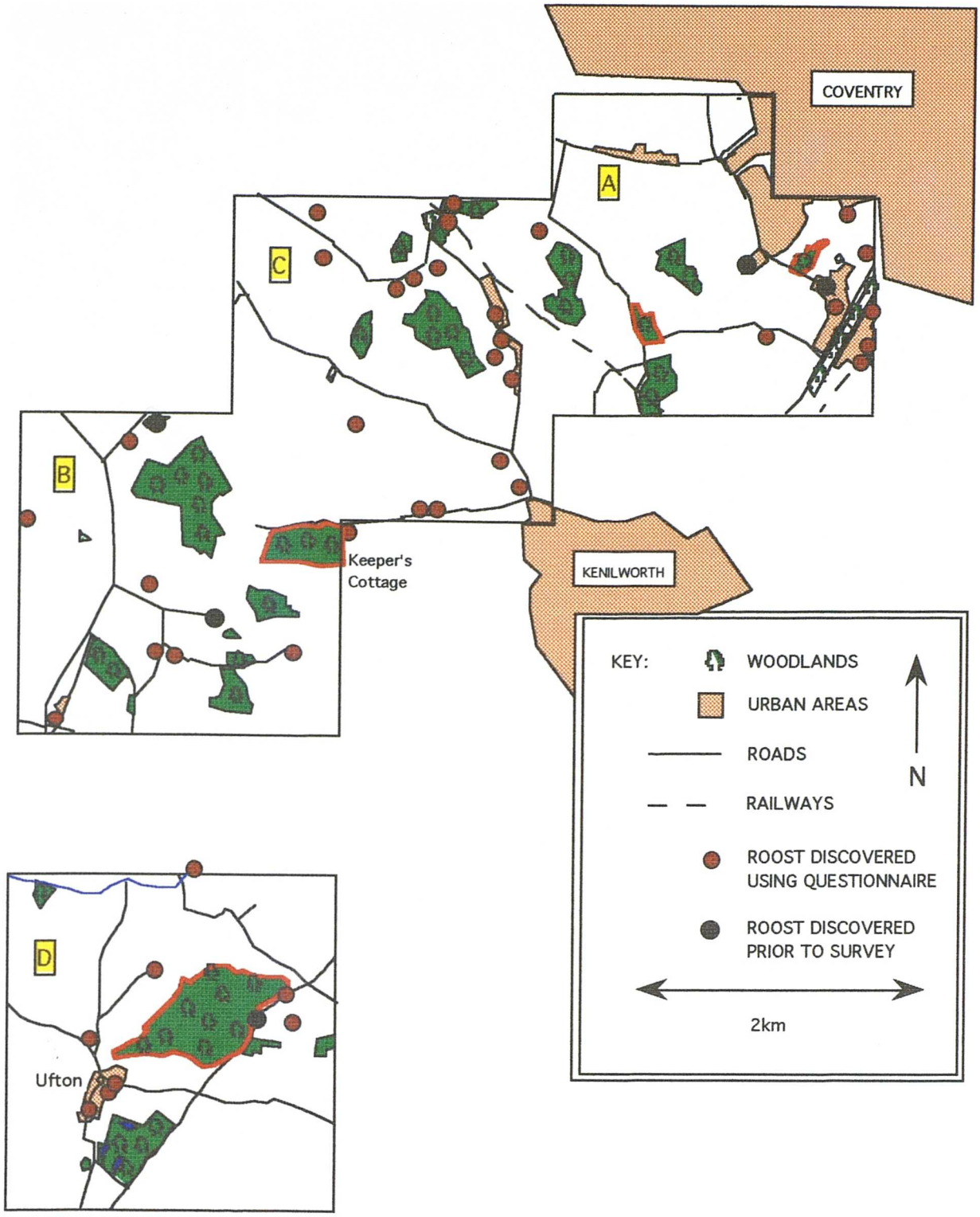


Fig 3.2 Questionnaire survey areas. Roosts located using questionnaires shown in red, roosts located prior to survey shown in black. Woodlands used for field work outlined in red.

- **Area C** ($8km^2$) connects the above two. It covers the northerly outskirts of the town of Kenilworth. Although most of the land in this area is agricultural, housing density is quite high, particularly along roads. There are several farmhouses and Chase Wood is situated slightly to the south of C.

- **Area D** ($9km^2$) is isolated from the above sectors by approximately 12km. Long Itchington-Ufton Wood is situated within this area and Ufton Village is fairly central to D. Ufton Village consists mainly of old houses along with a few small modern housing developments. The Grand Union Canal runs along the north border. Apart from A, this is the only area with a substantial waterway included. Land is agricultural, although a large proportion is taken up with two woodlands, Long Itchington Wood and Ufton Fields Nature Reserve (See Fig 3.2). Fields are often very large, hedgerow removal appears to have affected this area more than the above three.

3.2.2 Survey questionnaire: design

The questionnaire used in 1994 was modified slightly in 1995 (Figs 3.3 & 3.4). By reducing the number of open questions and increasing the number of tick response boxes it was hoped that the return rate would be improved in 1995. The questionnaire was presented on one A4 page. The objective was focused and questions were phrased simply so that they could be answered by all literate recipients (Bourque and Fielder, 1995).

The questionnaire incorporated the following features:

- a bat logo

  This may have stimulated readers' curiosity and reduced the chances of the leaflet being discarded unread.

- a University letter-heading

To reassure the recipient that the survey was bona-fide.

- a clear, simple title
- a box containing concise information about bats

  This was used as both an educational tool and to reassure roost owners who may have been nervous about bats roosting on their property. It also served to reassure respondents that the survey was conducted by knowledgeable surveyors.
- a request for information
- an offer to provide advice about bats
- a plea for nil responses to be returned
- tick boxes (in the second version)

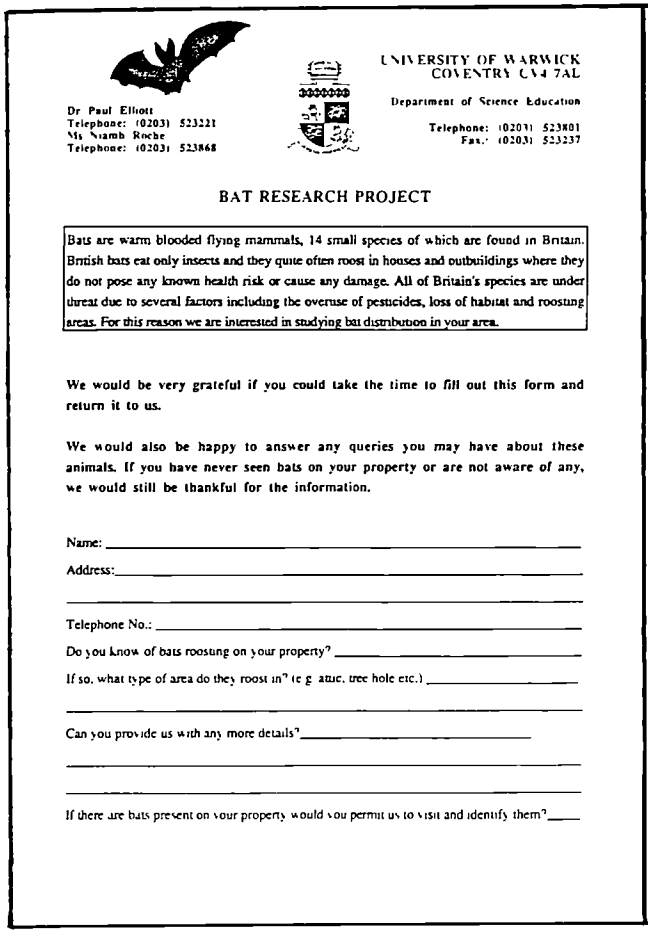
  These minimise the effort required to respond.
- a space to provide additional information
- a request for permission to make a follow up visit
- the whole sheet reverse folded to form the return envelope (Fig 3.5)
- postage paid

  Stamps were affixed to each questionnaire so respondents would not have to incur expenditure for returning it and may even have felt obliged to do so.

3.2.3 *Questionnaire delivery*

One copy of the questionnaire was hand delivered to every inhabited building, including all business premises and churches in the study areas. Questionnaires were delivered to A and B during the summer of 1994 and in 1995 to C and D.

Respondents claiming to have roosting bats on their property were telephoned and, where possible, visited in an attempt to validate their claim and identify the species concerned.



UNIVERSITY OF WARWICK
COVENTRY CV4 7AL

Department of Science Education

Dr Paul Elliott
Telephone: (0203) 523221
Ms Niamh Roche
Telephone: (0203) 523868

Telephone: (0203) 523801
Fax: (0203) 523237

BAT RESEARCH PROJECT

Bats are warm blooded flying mammals, 14 small species of which are found in Britain. British bats eat only insects and they quite often roost in houses and outbuildings where they do not pose any known health risk or cause any damage. All of Britain's species are under threat due to several factors including the overuse of pesticides, loss of habitat and roosting areas. For this reason we are interested in studying bat distribution in your area.

We would be very grateful if you could take the time to fill out this form and return it to us.

We would also be happy to answer any queries you may have about these animals. If you have never seen bats on your property or are not aware of any, we would still be thankful for the information.

Name: _____

Address: _____

_____

Telephone No.: _____

Do you know of bats roosting on your property? _____

If so, what type of area do they roost in? (e.g. attic, tree hole etc.) _____

_____

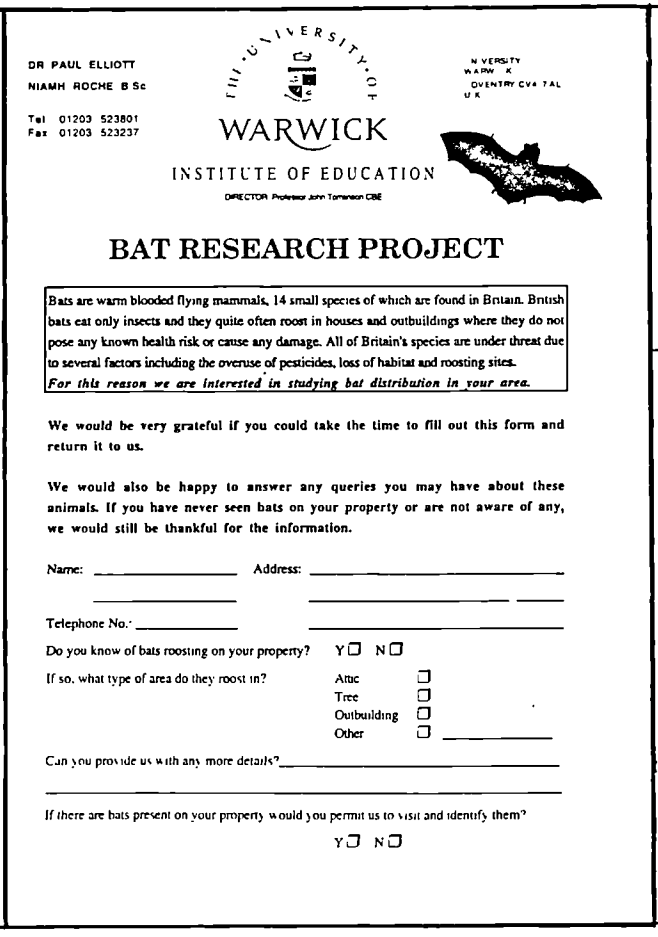
Can you provide us with any more details? _____

_____

_____

If there are bats present on your property would you permit us to visit and identify them? ____

Fig 3.3 Questionnaire used in 1994



DR PAUL ELLIOTT
NIAMH ROCHE B.Sc

Tel 01203 523801
Fax 01203 523237

THE UNIVERSITY OF
WARWICK
INSTITUTE OF EDUCATION
DIRECTOR Professor John Tomlinson CBE

UNIVERSITY
WARWICK
COVENTRY CV4 7AL
U.K.

BAT RESEARCH PROJECT

Bats are warm blooded flying mammals, 14 small species of which are found in Britain. British bats eat only insects and they quite often roost in houses and outbuildings where they do not pose any known health risk or cause any damage. All of Britain's species are under threat due to several factors including the overuse of pesticides, loss of habitat and roosting sites.
For this reason we are interested in studying bat distribution in your area.

We would be very grateful if you could take the time to fill out this form and return it to us.

We would also be happy to answer any queries you may have about these animals. If you have never seen bats on your property or are not aware of any, we would still be thankful for the information.

Name: _____ Address: _____

_____ _____

Telephone No.: _____ _____

Do you know of bats roosting on your property? Y☐ N☐

If so, what type of area do they roost in? Attic ☐
Tree ☐
Outbuilding ☐
Other ☐ _____

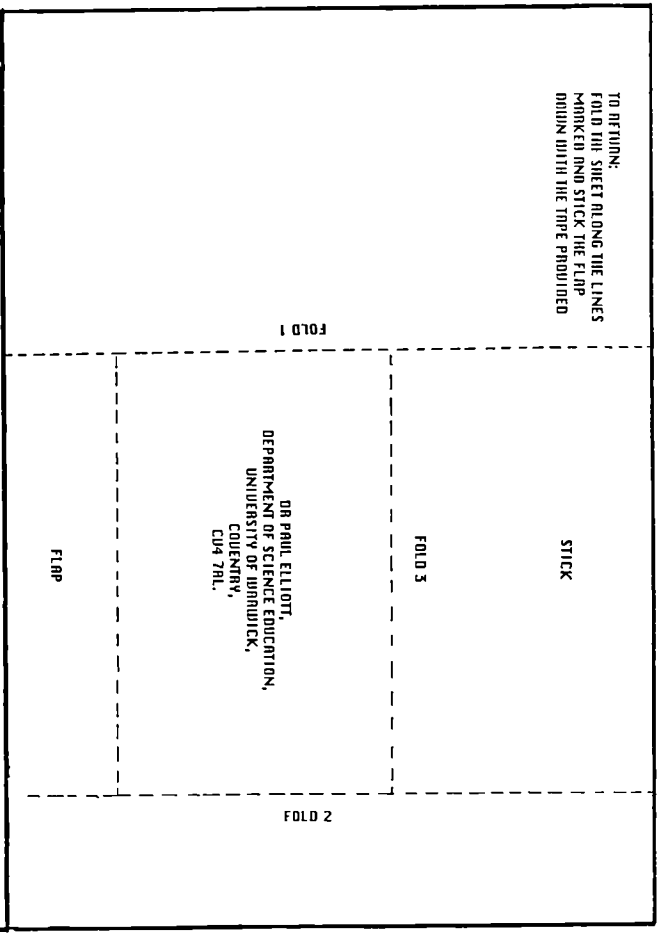
Can you provide us with any more details? _____

_____

If there are bats present on your property would you permit us to visit and identify them?

Y☐ N☐

Fig 3.4 Questionnaire used in 1995



TO RETURN:
FOLD THE SHEET ALONG THE LINES
MARKED AND STICK THE FLAP
DOWN WITH THE TAPE PROVIDED

FOLD 1

FLAP

DR PAUL ELLIOTT,
DEPARTMENT OF SCIENCE EDUCATION,
UNIVERSITY OF WARWICK,
COVENTRY,
CV4 7AL.

FOLD 3

STICK

FOLD 2

Fig 3.5 Reverse side of questionnaire

3.2.4 Roost ringing and counting

At Chase Wood (Keeper's Cottage roost, see Fig 2.6a) in 1996, ringing was carried out on female (one male) 45kHz *P. pipistrellus* under licence from English Nature. Bats were caught in a static hand net held over an emergence hole. Ringing was carried out from April to July 1996 on 10 nights (weighing and no ringing carried out on two extra nights).

The rings used were 2.5mm aluminium alloy bat rings provided by the Mammal Society. White reflective tape was stuck to the outside of the ring using Superglue adhesive. The sides of the tape were smoothed using fine sand paper to help prevent the tape being chewed off (A. C. Entwistle, pers. comm.).

One ring was placed on the left forearm of female bats and squeezed almost shut while ensuring the ring retained free movement along the radius. Red tape was used for males, however, only one adult male was captured during the study.

Bats caught emerging were weighed, forearm length was measured, and general condition was noted. Occasionally bats were recaptured during the season and the tape had disappeared from the ring. In these cases the original ring was removed from the bat's wing and replaced with a new one. In late May, females below 4.5g in weight were not ringed. Poor weather conditions had delayed pregnancy so the extra stress of ringing was not placed on bats of low weight.

3.2.4.1 Roost counts and mark-recapture population estimates

Roost emergence counts took place at Keeper's Cottage on 7 nights when no hand netting was being carried out and 4 nights simultaneously with hand net captures, from mid June until late July, 1996. On nights when no hand netting was being carried out, disturbance to emerging bats was kept to a minimum.

Numbers were counted (totalled every ten minutes) and strong torchlight (the beam of which pointed away from the roost) was used to determine whether the emergent bat had been ringed or not.

3.2.4.2 Mark-recapture techniques

Ringing was carried out at Keeper's Cottage, originally with the intention of observing bats from that particular roost in different woodland microhabitats. While observations were being made on emerging bats and counts of ringed bats taking place, it was decided to estimate the population of female pipistrelles associated with the roost. Bats were ringed during the season and small numbers periodically recaptured in hand nets. Also, emergence was counted on seven nights with no hand-netting.

This provided two possible ways of calculating population. Either with recaptures in the hand net or observations of emerging ringed bats.

The mark-recapture method consists of taking a random sample from a population, marking the individuals, and releasing them. After a period of time a second sample is taken and the number of unmarked and marked individuals counted. If there are no gains or losses to the population during the time interval, and both samples consist of 100 individuals, the proportion of marked individuals in the second sample is an estimate of the percentage of the total population that the initial sample made up (Poole, 1974).

All mark-recapture sampling methods require the use of a model to determine populations. This means that there are always conditions or assumptions associated with their use. The simplest model used in mark-recapturing is the Lincoln or Peterson index. Most mark-recapture indices, including the Lincoln index, are constrained by the following conditions:

1. *Animals carrying marks must not suffer higher mortality than those not carrying marks.* It was not assumed that ringed animals would suffer higher

mortality than unringed animals. Ringing was carried out under licence from English Nature by trained individuals in order to minimise risk to animals. No animals subsequently caught in hand nets were thought to be distressed or in poor condition due to a ring.

2. *Once released, marked animals must mix at random within the study population.* From observations or emerging bats it could be seen that ringed and unringed individuals were mixed.
3. *Marked animals must be no more or less easily captured or observed than unmarked 'naive' animals.* It was possible that ringed animals avoided subsequent capture in the hand net, thus preventing an accurate determination of colony size using hand net recapture data. However, it was assumed that observing the numbers of marked animals emerging from the roost, along with the number of unmarked individuals, would not be prone to the same bias. Observation counts of emerging animals were aided by the use of bat detectors and, on all occasions, at least two people noted numbers and ringing status.
4. *Marks must not be lost or overlooked in samples.* This was the most difficult assumption to overcome in the study given the fact that several ringed individuals were caught in July and tape had disappeared from their rings. There was probably continuous decay of tape from rings due to Superglue becoming brittle and fracturing and bats chewing at the rings. A gradual decline in the numbers of ringed animals with reflective tape means that population may be slightly overestimated (if less ringed bats are noted emerging than are actually ringed).
5. *Some models permit no additions or deletions to the population through birth immigration, death and/or emigration during the study period.* The possibility of births affecting the population was minimal until late July. At this time, newly volant young were probably emerging with adults. However,

emigration was not quantifiable. Given the results shown in Table 3.4 it seems unlikely that emigration from the roost was taking place in July.

6. *The samples were taken randomly and all individuals were equally available for capture.*

adapted from Poole (1974), and Thomas and La Val (1988).

Thomas and La Val (1988) warned of ignoring the various biases and assumptions of models when undertaking studies (e.g. a number representing the population).

In order to determine the true size of the population the estimate of recaptures was made using a count of emergent ringed bats rather than the number of ringed bats caught in a hand net.

The numbers of emerging unringed and ringed bats were entered into the following adapted version of Lincoln's equation:

$$x=an/r$$

where

- a is the total number of bats noted emerging in one evening
- n is the total number of marked animals in the area
- r is the number of emerging bats noted to be ringed

12 hand net marking and recapturing instances took place, between 19th April 1996 and 1st August 1996. On four of these nights emergence counts were also carried out, with bats' ringing status noted. On 7 other nights from 26th June until 31st July emergence counts only were carried out. This minimised the disturbance to emerging bats which may have prevented individuals from exiting in the usual manner.

Data on the number of ringed and non-ringed bats from emergence counts were entered into a table and population was estimated from the above equation. Variance of estimates, or confidence intervals, are easily calculated from the above equation when only one mark-recapture instance is

used. However, computing variance becomes more difficult with an increased number of mark-recapture instances and true confidence interval estimation is not possible (Poole, 1974; Smith, 1980). For this reason, no confidence intervals were calculated for the estimates.

3.3 Results

3.3.1 Questionnaire

In total, 809 questionnaires were delivered. Of these 389 were returned, representing 48% of those delivered. The number of reported roosts was 69 while the number of confirmed roosts was 39.

In some instances it was impossible to arrange a follow up visit, usually because of a reluctance on the part of the house owner to allow strangers to visit, but possible to confirm the presence of a roost by telephone interview. In a few cases respondents had reported the presence of roosting bats but it became apparent on speaking to them that this claim was not supported by any evidence and that they had simply seen bats on the wing in the vicinity and assumed that they must be roosting nearby. Alleged roosts were confirmed by site visit or telephone interview.

During visits it was not always possible to confirm the identity of species involved. Sometimes the roost was inaccessible or the animals not present at that time. However, in many of these cases it was possible to use evidence such as the nature of faeces, their distribution and the roost's location to infer species identity.

Return rates in 1994 and 1995 did not vary greatly despite the slightly different questionnaires used. In fact, return rates were slightly lower for the modified (1995) questionnaire. This may have been due to a lower level of motivation to respond in 1995. In 1994 a press release had been made about

the search for bat roosts and local press attention may have resulted in improved response rates. The timing of mail shots is an important consideration for any survey (Bourque and Fielder, 1995).

For bats, mid-summer is probably the best time of year to launch a survey because residents are more likely to be aware of their presence. It is also necessary to be mindful of public opinion regarding the topic in question (Bourque and Fielder, 1995). Had the questionnaires been delivered during the same time as the rabies 'scare' in 1996 (e.g. Eastcott, 1996) the overall response rate may have been lower or much more negative towards bats.

3.3.2 Analysis of questionnaire results

The survey revealed 39 previously unknown roosts sites in the study areas (see Fig 3.2). 7 in area A, 7 in area B, 18 in area C and 7 in area D. This represents 10% of returns and 4.8% of all delivered questionnaires. A breakdown of the roost types both reported and confirmed is provided in Table 3.1.

Table 3.1 **Reported bat roosts**

Roost type	No. of reported roosts	No. of confirmed roosts
Roof space, e.g. attic, loft	41	30
Outbuilding, e.g. barn, cow shed	16	8
Tree	12	1

Table 3.2 **Identity of roosting species**

Species	Number of roosts
Pipistrellus pipistrellus - present	3
P. pipistrellus - suspected (faecal evid.)	8
Plecotus auritus - present	3
P. auritus - suspected (faecal evidence)	10
Species not identified	15

Anything below a 100% return rate generates problems for the analysis of results. It is known that response rates are usually higher from rural areas than from cities (Fowler, 1984). It is likely that people who have a particular interest in the subject matter or research itself are more likely to return the questionnaire than those who are less interested (Fowler, 1984). Therefore, a factor motivating some respondents to return the questionnaire may be that they are in a position to do so positively by reporting a roost. If this is the case, then there may be a lower incidence of roost sites among the properties from which there was no response.

Alternatively, perhaps it should be assumed that all non-returns would show a similar incidence of roosts to returns. If this assumption is made, then it alters the overall roost density figure from 1.15 to 2.4.km^{-2}. This compares with a total confirmed roost density of 0.124.km^{-2} in a study in northern England (Jones *et al.*, 1996). However, the study by Jones *et al.* included highlands and areas of sparse human population, while the English Midlands are both low-lying and densely populated by humans.

Return rates in A and C, the two areas with most dense human populations, were lower than the other two areas (44% and 40% compared with 65% and 55%) (Table 3.3).

Table 3.3 **Questionnaire results in each area**

Area	Response rate	Housing density (km^{-1})	Roost density (from survey only) (km^{-1})	Roost density from all records (km^{-1})	Pipistrelle roost density from all records (km^{-1})	Long-eared roost density from all records (km^{-1})
A	44%	41.25	1.14	1.5	0.625	0.375
B	65%	7.67	0.78	1.1	0.33	0.67
C	40%	37.5	2.13	2.13	0.5	0.5
D	55%	12.22	0.78	0.89	0.22	0.44

This may have been due to a lack of interest in or knowledge about wildlife among more urban communities. However, the density of roosts located using the survey was higher in areas A and C than in B and D. This may correlate with a preference, among pipistrelles, for roosting in modern houses.

3.3.3 Results from bat ringing and roost counts

A total of 79 individual pipistrelles were ringed from April to July 1996 at Keeper's Cottage, Kenilworth. 78 of these were females, 30 of which were recaptured from mid-May to August. Of these 30, 9 were recaptured with little or no reflective tape remaining on the aluminium ring. In 8 of these cases, a new ring was placed on the bat's forearm. The ninth was recaptured on the final night of field work and the ring was not changed. The low level of recaptures in hand nets may have been because of trap shyness.

The mark-recapture technique on this occasion did not rely on physical recaptures, rather the observation of numbers of bats emerging from the roost in Chase Lane and the numbers emerging that were actually ringed.

Two factors affecting colony size estimates from mark-emerging counts are: the decay of tape from rings, and the possibility that migration to or from the roost occurred during the study. However, a similar number of

individuals were calculated as making up the colony on 6 nights between 27/6 and 23/7 (Table 3.4). This number varied between 111 and 118 individuals, while the maximum number of bats counted during a dusk emergence was 94 on 26/6. On 16/7 and 23/7, mark-observation data resulted in an estimate of total colony size at 115 individuals. This low variability suggests that there is little migration and that the effects of tape decay were negligible, at least during that time period. If, however, decay of reflective tape was occurring, 115 may be an overestimation of the number of individuals associated with the roost at that time. The average number of emerging bats during this study (observed on 7 nights without disturbance by netting) was 82.5.

From 25/7 an increase in estimated colony size was noted and this was assumed to indicate emergence of newly volant young (Table 3.4).

Table 3.4 **Mark-emergence results using Lincoln's Index**

Date	Total emergence (A)	Total no. marked animals in area (B)	AxB	Sum of AxB	No. ringed bats emerged	Sum ringed bats emerged (C)	AxB/C Estimated Population
19/6[1]	77	37	2849	2849	27	27	195.5
20/6[1]	68	44	2992	5841	17	44	132.8
26/6	94	44	4136	9977	35	79	126.3
27/6	90	44	3960	13937	39	118	118.1
4/7	82	48	3936	17873	43	161	111
10/7[1]	76	65	4940	22813	32	193	118.2
11/7	82	65	5330	28143	53	246	114.4
16/7	77	65	5005	33148	42	288	115.1
23/7	70	65	4550	37698	39	327	115.3
25/7[1]	61	75	4575	42273	20	347	121.8
31/7	115	75	8625	50898	45	392	129.8

The average time of first emergence from the roost (from seven nights during pregnancy, lactation and weaning) was 3 min after sunset. This

[1] Netting was carried out simultaneously with roost emergence counting and this may result in inaccurate population estimates for those nights

compares with time of first emergence calculated for *P. pipistrellus* by Jones and Rydell (1994) of 27 minutes after sunset.

3.4 Discussion

3.4.1 Questionnaire

The return rate was very good for an unsolicited questionnaire (Fowler 1984). This suggests that the incorporated design features had the desired effect. A high level of public interest in wildlife and conservation probably aided the survey. However, 52% of questionnaires were not returned. Possible reasons for no response include:

- apathy
- too busy
- a fear and/or general dislike of bats
- lack of knowledge or awareness of bats in the area
- knowledge of the presence of bats on property but reluctance to initiate a chain of events that could result in a visit from a stranger
- fear of legal implications of having roosting bats on property
- reluctance to reveal information to a stranger (telephone no. etc.)
- illiteracy

By revising and refining the design of the questionnaire it may be possible to reduce these negative influences. Including a statement promising that the responses would be confidential may have reassured some recipients worried about the implications of having roosting bats on their property, for instance.

The technique is only effective for locating roosts in buildings (Table 3.1) and is therefore only useful for finding species that regularly utilise

buildings. Used in conjunction with other field methods, such as detector surveys, it becomes more beneficial.

The cost of the technique is not particularly high when compared to traditional field methods. Each roost cost approximately £17 plus time to locate and confirm. It is therefore a technique within the reach of bat groups and other voluntary organisations.

By means of the questionnaire sheet itself and during follow up visits and telephone calls, a great deal of information about bats and their conservation was conveyed to members of the public. A questionnaire survey could also therefore be described as a public relations exercise targeted specifically at people who are the custodians of bat roost sites. Relating a positive attitude to house owners towards bats must be a key element in bat conservation efforts.

3.4.1.1 Population density

Speakman *et al.* (1991) calculated the average number of *P. pipistrellus* km^{-2} by multiplying the average number of individuals associated with each roost (117) by the number of known roosts to obtain a minimum population for the species. To estimate the density of bats, minimum population was divided by the area of occupied 5x5km squares. By doing this they calculated a density of pipistrelles at 18.2 bats km^{-2}. In this study, the number of pipistrelle roosts found in the $25km^2$ that made up the three adjacent survey areas (A,B&C) was much higher (12). Even if the lower average number of pipistrelles per roost from Jones *et al.* (1996) is used to calculate a minimum density (69.6) the result is still much higher, 33.4 bats km^{-2}. It is possible that pipistrelles roost in lower numbers in Midlands England and if this is the case density is also lower.

Average roost sizes for *P. auritus* calculated in Scotland and northern England are the same, 16.8 bats per roost (Jones *et al.*, 1996; Speakman *et al.*,

1991). If the same roost size is applied to the three questionnaire areas (A,B&C), this results in a density of 8.7 bats km^2, at least four times the estimates from northern England or Scotland (1.04 and 1.66 km^{-2}, respectively).

These results indicate that density of bats may be much higher in the English Midlands than in more northerly regions of Britain. However, more roost counts and validations of roost occupancy should be carried out to verify this hypothesis.

3.4.1.2 Species located

The relative density of pipistrelle and long-eared roosts differed in each area. Supporting Jones *et al.* (1996), there appears to be a reduction in long-eared roost density with increased urbanisation, and an increase in pipistrelle roost density with urbanisation.

The most commonly encountered roost type was that of *P. auritus*. Most of the roosts discovered were in houses over 100 years old. Almost all had attics divided into several compartments. *P. auritus* may be the first bats discovered from a questionnaire survey their roosts are usually covered with a scattering of droppings, thereby alerting roost owners to their presence. Other species such as the pipistrelle do not usually roost in such an obvious manner and many house owners remain ignorant of their presence.

No confirmed *Myotis* spp. roosts were recorded as a result of the survey, although it is possible that a few of the unidentified or unconfirmed sites were of *M. mystacinus*/*M. brandtii*. 20% of observed bat passes recorded in the four study woodlands were from *Myotis* spp (see section 4.3.1).

A possible whiskered/Brandt's roost was located in Tocil Wood during a detector survey in July 1995. Perhaps they are making greater use of trees

than buildings. A greater number of follow up visits at dusk and dawn may result in more species being recorded.

M. daubentonii were considered unlikely to be common except in area A where they have been detected foraging over the small lakes adjacent to Tocil Wood. A 16 year long survey campaign with varying intensity in Scotland (based around two major rivers) revealed 184 bat roosts of which only 4 were Daubenton's despite the proximity of large waterways (Speakman *et al.*, 1991).

In Area A, the results may be somewhat biased given that the researchers are based in this area and additional roosts have been located as a result of field work there.

3.4.2 Roost counts and ringing

3.4.2.1 Roost numbers

The average number of emerging pipistrelle bats during this study was 82.5. This is slightly above the average number of pipistrelles counted out of roosts in northern England by Jones *et al.* (1996) (69.6 bats) and lower than that recorded by Speakman *et al.* (1991) in Scotland (117 bats). However, roost counts were carried out at two other known roost sites from the questionnaire survey areas in 1994 and 1995 and these two averaged only 28.5 individuals each, this suggests that the Keeper's Cottage roost is particularly important in the area.

The colony number calculated from mark-emergence counts suggests that approximately 115 individuals are associated with the roost. However, this may be an overestimation due to a loss of reflective tape marks during the season. Swift (1980) noted that during May and early June colony size was very variable but had stabilised by late pregnancy. This pattern was similar in Kenilworth where colony size estimates were more variable from early to mid-June but stabilised at around 115 individuals by late June.

3.4.2.2 Emerging young

Maier (1992), recorded young becoming volant at a pipistrelle roost in Oxford in mid-July. Swift (1980), noted young at colonies in Scotland becoming volant in the last week of July with all the young weaned by August 19.

The weather in early summer, 1996, was particularly cool and this may have resulted in delayed pregnancies (e.g. Racey 1973; Racey *et al.*, 1987) and young not becoming volant until late July (from 25th July onwards), similar to Scotland. May 1996 in Coventry was the coldest on record since 1968 (Bablake Weather Station, (BWS)). June was also a cold month with an average monthly temperature of 15.2°C.

3.4.2.3 Emergence times

P. pipistrellus average time of first emergence was found by Jones and Rydell (1986) to be 21 minutes after sunset, and median emergence time was 33 minutes after sunset. Swift (1980) recorded the time of first emergence of pipistrelles in three roosts in Scotland as 35 minutes after sunset.

In this study, mean emergence time (from seven nights during pregnancy, lactation and weaning) was 3 minutes after sunset. Median time of emergence (calculated as the mid-way point of emergence) was 20.43 minutes. A major factor contributing to earlier emergence times in this study compared with those noted by Jones and Rydell (1994) and Swift (1980), is probably the proximity of woodland to the roost. Bats emerged on the woodland side of the house (as far as is known) and usually flew directly to it.

Jones and Rydell (1994) noted that the time of emergence reflected the light level a bat was prepared to tolerate They observed that early fliers also feed in relatively open habitats while those that fly out later more often fly under tree canopies. Some bats avoid exposed and open habitats until

darkness falls, instead concentrating their initial foraging activities at dusk to more protected areas near vegetation. The pipistrelles in this study probably availed of the proximate tree canopy to emerge earlier and exploit insects in the woodland.

Summary

The questionnaire method resulted in the discovery of many roosts in survey areas. Return rates of the questionnaire and resulting roost densities were both relatively high. Marked pipistrelles were examined emerging from a roost and young were estimated to become volant from 25th July onward. The time of emergence from this roost was earlier than average because of the proximity of sheltering woodland.

Chapter 4

USE OF DECIDUOUS WOODLAND MICROHABITATS BY *PIPISTRELLUS PIPISTRELLUS* AND *MYOTIS* SPECIES

4.1 Introduction

Deciduous woodland has the richest invertebrate fauna of any habitat in Britain (Kirby, 1992) and provides important foraging and roost sites for many species of bat (Mayle, 1990a).

De Jong (1994) noted that deciduous woodlands were the favoured habitat of *P. pipistrellus*, while *M. brandtii* preferred coniferous woodlands. De Jong (1994), and Walsh *et al.* (1996 a&b) have studied woodlands in Sweden and Britain, respectively, and have focused on open areas within forests and woodland edges as important activity sites.

De Jong (1994), studying habitat use by bats in Uppsala, examined vegetation structures used by several common species including *P. pipistrellus* and *M. mystacinus*. One of the features used most by *P. pipistrellus* was the edge habitat between forests and open spaces. The open spaces themselves were significantly avoided by *P. pipistrellus*. However, *M. mystacinus* avoided edges and preferred foraging within forest. De Jong found that no species foraged in dense forest but most species used relatively open forest.

Given the wing morphology and echolocation of *P. pipistrellus* it is hypothesised that these bats will be most active in woodland microhabitats that range from open to mildly cluttered, but not in dense clutter.

Walsh *et al.* (1995), surveying bats in the British landscape, found that open areas within woods and broadleaved woodland edges were sites of high bat activity. Both woodland edges and openings within woods were selected and, of these, edges were preferred to openings (Walsh & Harris, 1996a).

High insect availability may be a reason for the preference found among bats for edges (de Jong, 1994; Walsh and Harris, 1996a). However, Kalcounis and

Brigham (1995) found a higher insect abundance in clutter compared with open areas.

A preference for edges may be related to the use of linear landscape features by commuting bats (Limpens and Kapteyn, 1989). If this is the case, then it is hypothesised that edges may be preferred early during the night (around dusk) and not selected later in the evening.

Kalcounis and Brigham (1995) found that heavier *M. lucifugus* foraged in less cluttered areas than lighter individuals of the same species. They suggested that this was because bats of higher mass have higher wing loading (wing loading is the ratio of body mass to wing area) and are, therefore, less manoeuvrable. In this study, it is hypothesised that there may be a change in the use of woodland microhabitats during the season. The only areas of woodland available to pregnant females may be open habitats.

4.2 Methods

4.2.1 Field work and sites

For descriptions of study sites, field work nights, bat activity and insect abundance measurements see Chapter 2.

4.2.2 Vegetation density

Vegetation density was estimated using several methods in July 1996. Cover abundance of shrub and canopy layers were assessed in each microhabitat (average: one point every 15m). Cover abundance was estimated by eye (%). Measurements of vegetation density were taken by the same person in each wood in order to preserve consistency.

Vegetation density in each microhabitat was estimated in July 1996 using a method adapted from Bellamy, Hinsley and Newton (1996). There were no visible canopy or shrub layer changes in the sites between 1995 and 1996. Density of foliage in the canopy (>5m) and shrub layers (2-5m) were estimated by eye using five density classes numbered 0 to 4, where 0 = no vegetation and 4 = very dense (or foliage takes up 75-100% space) vegetation. In each microhabitat the proportion of area attributable to each density class was recorded at several points and the average proportions for each density class for each layer were combined to give the following index for each microhabitat

$$D = \sum_{s=0}^{4} P_s s$$

where

- D is the density index
- P_s is the proportion of area attributed to each class, s.

The maximum possible index for each layer is 4 and the minimum is 0. Vegetation density of edge microhabitat shrub and canopy layers were taken to be zero.

4.2.3 Analysis of results

4.2.3.1 Chi-square test

Observed bat activity (total number of bat passes from each microhabitat) from 1995 and 1996 in each woodland microhabitat was analysed using a program to discern habitat preferences (based on a method outlined by Neu, Randall Byers and Peek (1978)). Data from each wood in 1995 were analysed separately because different combinations of microhabitats were studied in each.

The analysis is an adapted Chi-square test and involves the construction of confidence intervals at a specified significance level based upon observed bat activity (number of bat passes). These are also corrected to allow for several simultaneous estimates of activity (along a transect) using the Bonferroni, z, statistic. Assuming a uniform distribution of activity throughout the woodland, expected proportions of bat activity for microhabitats are calculated and compared with constructed confidence intervals.

If the expected proportion falls outside the confidence interval and below its lower limit, this is an indication that the microhabitat is preferred by bats. If the expected proportion falls outside the interval's upper limit this indicates that the microhabitat is avoided by bats.

The constructed interval is taken to be a robust estimation of preference or avoidance of a habitat providing $np \geq 5$ and $n(1-p) \geq 5$, where n is the total number of observations in each analysis and p is the theoretical proportion of occurrence (in this case the proportional length of transect of a microhabitat divided by total length of transect) (Hayes and Winkler, 1970).

1996 data from Chase Wood was also analysed using this method. However, because each microhabitat was examined from a stationary position, proportionate length of transect could not be used as an "expected" value. Instead, the proportion of time spent in each feature was the same so the "expected" proportion for each microhabitat in Chase Wood, 1996, was 0.1667.

Total number of passes (*P. pipistrellus* and *Myotis* spp.) for each woodland during 1995 were analysed using Chi-square. Number of passes (of pipistrelles) were also divided into beginning, mid-season, and end of the season. In this way changes in microhabitat use by pipistrelles during 1995 could be determined. To test the hypothesis that bats use edges as a flight path while commuting, pipistrelle data from the first transect covered each night in each woodland were

analysed using Chi-square and compared with the results of the same test using second transect data.

4.2.3.2 Nonlinear regression analysis of pipistrelle activity and vegetation levels

A simple example of a regression model is a straight line relationship between a pair of variables, denoted X and Y:

$$Y=\alpha+\beta X$$

where α and β are parameters (physical constants) linking Y and X.

- Y is the response or dependent variable
- X is the explanatory, predictor, regressor or independent variable

The above equation is a linear model as the relationship between the variables is linear. However, the following equation:

$$Y=aX^b$$

where a and b are parameters, describes a nonlinear model (Ratkowsky, 1990). This means that derivatives of Y with respect to a or b are functions of a or b. In the above equation the derivative of Y with respect to a and the derivative of Y with respect to b are both functions of a and/or b, so that this model is a nonlinear regression model (Ratkowsky, 1990).

4.2.3.2.1 Fitting a nonlinear regression model

There is no simple method for devising a well fitting model (Ratkowsky, 1990). With a single explanatory variable a plot of the data of Y versus X is matched up against graphs of various models in an attempt to find one that appears to fit the data set(s) (Ratkowsky, 1990). Unlike simple regression (see section 6.2.2.1), r^2 is not used as a measure of the proportion of explained variation. According to Ratkowsky (1990), r^2 should only be used when the

regression is a linear one and there is a constant term in the equation. Zar (1984) recommended the use of the F-value as a test of significance of the fit of a model.

The Y variable was *P. pipistrellus* activity (no. of passes per 100m per night) in different microhabitats. These were plotted against different measurements of vegetation density:

- cover abundance of shrub layer (%)
- cover abundance of the canopy layer (%)
- average of the two cover abundances (%)
- index of vegetation density of the canopy layer
- index of vegetation density of the shrub layer
- index of vegetation density of the two layers combined

Using distance weighted least squares smoothing (DWLS), plots were examined for structures which could potentially be described using mathematical functions. DWLS fits a line through a set of points by least squares. The surface is allowed to flex locally in order to make a better fit to the data and the DWLS function is a useful way to determine the shape of a relationship before carrying out regression analysis (Wilkinson *et al.*, 1992).

The fit of a model to activity/vegetation density data sets was carried out using the nonlinear model function of SYSTAT 5.2.1. A possible equation was entered, specifying the X (vegetation) and Y (bat activity) variables along with parameters to be estimated. In general, the estimation procedure used was Quasi-Newton (Fletcher, 1972). Iterations of the estimation procedure terminate when the displayed values of the parameter estimates in the iteration log fail to change (Wilkinson *et al.*, 1992).

Curvilinear and nonlinear model types, mainly from Ratkowsky (1990), were investigated as possible fits. These were

1. $Y=aX/X^2$

2. $Y=a/bX$
3. $Y=aX\exp(-bX)$
4. $Y=aX\exp(-bX^c)$
5. $Y=aX^b\exp(-X)$
6. $Y=1-\exp(-aX^2)$
7. $Y=a\cos(X+b)$
8. $Y=(a+bX)c^X$
9. $Y=X/(a+bX+cX^2)$
10. $Y=X/(a+bX+c\sqrt{X})$

where *a, b* and *c* were constants to be determined by SYSTAT. In all of the above equations the line is forced through zero. This was done in order to simplify the procedure. When the most accurate model(s) was (were) determined another parameter was entered into the model to define the intersect with Y.

Various combinations of data were used:

Y variable - pipistrelle activity from

- all four woodlands combined (1995)
- three woodlands excluding Long Itchington (1995)
- Chase Wood (1995)
- data from the first transect covered each night in Chase Wood (1995) (to provide an accurate comparison with 1996 data)
- Chase Wood (1996)
- Chase Wood activity (1996) without nights of full moon (as in 1995)

The X variable - a measure of vegetation density or cover

- index of vegetation density as described earlier
- % cover abundance

Data obtained on four nights in June and July 1995, and six nights from the same months in 1996, were used in nonlinear regression analyses.

4.3 Results

4.3.1 Overall activity in 1995 and 1996

A total of 3640 bat passes were recorded during the 51 nights of survey work in 1995. Of these, 70.22% were *P. pipistrellus* and 24.2% were *Myotis* spp. It is likely that most of the *Myotis* spp. calls were from *M. mystacinus/brandtii* because they have relatively loud echolocation calls (Stebbings, 1993), they often forage in woodland (Corbet and Harris, 1991) and they have been frequently recorded in Warwickshire (WBRC). The remaining 5.58% of observed bat passes were from *N. noctula*, *P. auritus* and unidentified species. These proportions are similar to those observed in the national bats and landscapes survey where 71% of bat passes were identified as *P. pipistrellus* and 17% were identified as *Myotis* spp. (Walsh *et al.*, 1995).

The two phonotypes of *P. pipistrellus* were distinguished from late July 1995 onwards and of the 1194 *P. pipistrellus* passes recorded from then, only 9.8% were the 55kHz type. All computations involving *P. pipistrellus* include both phonotypes unless otherwise indicated.

509 bat passes were observed in Chase Wood during the eleven nights of surveying from late May to July 1996. Of these, 84% were *P. pipistrellus* and 8% were identified as *Myotis* spp.

4.3.2 Comparisons of activity between woods in 1995

A single factor ANOVA was carried out comparing the number of bat passes per 100m transect per night in each of the woods. Results show that overall bat activity was the same in each woodland ($F_{(df3, 45)}$=0.30, p=0.82).

Close to zero *P. pipistrellus* activity was recorded during the first three nights of data collection in Long Itchington, Roughknowles and Tocil Wood and the first two nights in Chase Wood. In order to achieve the requirements for normality for ANOVA testing, these data were removed from analysis. No significant difference in average *P. pipistrellus* passes per 100m of transect was found between woods ($F_{(df3, 36)}$=2.11, p=0.12).

The same test on *Myotis* spp. data could not be carried out as distributions of each of the samples were found to deviate significantly from normal. A non-parametric test, Kruskall Wallis, was used instead and no significant difference was found in sum of ranks between woods (Kruskall Wallis test $statistic_{(n=51)}$= 5.51, p=0.14).

A comparison was made of pipistrelle activity in preferred microhabitats of woodlands. Roughknowles had significantly lower *P. pipistrellus* activity in microhabitats for which a preference was shown (Open woodland 1&2, Table 4.2) compared with preferred microhabitats of two of the other study sites (Natural glades, Tables 4.1 and 4.3) (Kruskall Wallis $_{(n=75)}$=12.57, p<0.01), Chase and Tocil. It was also found that less *P. pipistrellus* activity was observed in preferred microhabitats of Long Itchington (Woodland 1&2, Table 4.4) compared with preferred microhabitats along transects in Chase and Tocil.

4.3.3 Use of woodland microhabitats by bats

Significant Chi-squares showed that *P. pipistrellus* and *Myotis* species were not using each woodland microhabitat in proportion to its availability along a

transect (Tables 4.1 to 4.5). Results showed a pattern of use that was followed in each wood.

Table 4.1 **Analysis of *Pipistrellus pipistrellus* and *Myotis* spp. activity in different microhabitats of Tocil Wood, 1995**

	Pipistrellus pipistrellus $\chi^2 = 496.76^{***1}$				*Myotis* spp. $\chi^2=33.66^{***}$			
Micro-habitat	Observed prop. of ***P. pip.*** passes (n=755)	Expected prop. of ***P. pip.*** passes	Confidence interval (95%)	Selec.	Observed prop. of ***Myo.*** passes (n=138)	Expected prop. of ***Myo.*** passes	Confidence interval (95%)	Selec.
Natural glade	0.22	0.06	0.18-0.26	+	0.12	0.06	0.05-0.20	=
Woodland	0.22	0.24	0.18-0.26	=	0.34	0.24	0.23-0.45	=
Ride (lit by white lights)	0.24	0.14	0.20-0.28	+	0.19	0.14	0.10-0.27	=
Dense vegetat. 1[a]	0.09	0.13	0.06-0.12	-	0.12	0.13	0.04-0.19	=
Dense vegetation 2	0.1	0.13	0.07-0.128	-	0.08	0.13	0.02-0.14	=
Edge	0.13	0.31	0.15-0.17	-	0.15	0.30	0.07-0.23	-

Table 4.2 **Analysis of *Pipistrellus pipistrellus* and *Myotis* spp. activity in different microhabitats of Roughknowles Wood, 1995**

	Pipistrellus pipistrellus $\chi^2= 138.29^{***}$				*Myotis* spp. $\chi^2=33.66^{***}$			
Micro-habitat	Observed prop. of ***P. pip.*** passes (n=421)	Expected prop. of ***P. pip.*** passes	Confidence interval (95%)	Selec.	Observed prop. of ***Myo.*** passes (n=85)	Expected prop. of ***Myo.*** passes	Confidence interval (95%)	Selec.
Open woodland 1	0.51	0.40	0.45-0.57	+	0.74	0.40	0.62-0.86	+
Open woodland 2	0.2	0.08	0.15-0.25	+	0.08	0.08	0.00-0.14	=
Dense vegetation	0.06	0.06	0.03-0.09	=	0.09	0.06	0.02-0.17	=
Edge	0.23	0.46	0.18-0.28	-	0.09	0.46	0.02-0.17	-

[1] see List of Abbreviations for explanation of *, ** and ***

Table 4.3 **Analysis of *Pipistrellus pipistrellus* and *Myotis* spp. activity in different microhabitats of Chase Wood, 1995**

	Pipistrellus pipistrellus χ^2= 614.78***				*Myotis* spp. χ^2=444.19***			
Micro-habitat	Observed prop. of ***P. pip.*** passes (n=681)	Expected prop. of ***P. pip*** passes	Confidence interval (95%)	Selec.	Observed prop. of ***Myo.*** passes (n=323)	Expected prop. of ***Myo.*** passes	Confidence interval (95%)	Selec.
Natural glade	0.16	0.03	0.12-0.20	+	0.19	0.03	0.13-0.25	+
Clear-felled glade	0.09	0.07	0.06-0.12	=	0.06	0.07	0.02-0.09	=
Open woodland	0.17	0.22	0.13-0.21	-	0.15	0.22	0.10-0.21	-
Woodland	0.29	0.16	0.24-0.33	+	0.32	0.16	0.25-0.39	+
Dense vegetation	0.05	0.10	0.03-0.08	-	0.13	0.10	0.08-0.17	=
Edge	0.24	0.44	0.20-0.28	-	0.15	0.44	0.10-0.20	-

Table 4.4 **Analysis of *Pipistrellus pipistrellus* and *Myotis* spp. activity in different microhabitats of Long Itchington Wood, 1995**

	Pipistrellus pipistrellus χ^2= 257.53***				*Myotis* spp. χ^2=73.69***			
Feature	Observed prop. of ***P. pip.*** passes (n=552)	Expected prop. of ***P. pip.*** passes	Confidence interval (95%)	Selec.	Observed prop. of ***Myo.*** passes (n=335)	Expected prop. of ***Myo.*** passes	Confidence interval (95%)	Selec.
Clear-felled glade	0.19	0.15	0.12-0.20	=	0.04	0.15	0.01-0.07	-
Woodland 1	0.15	0.10	0.11-0.19	+	0.16	0.10	0.11-0.21	+
Woodland 2	0.40	0.18	0.34-0.45	+	0.30	0.18	0.24-0.37	+
Ride	0.13	0.19	0.10-0.17	-	0.19	0.19	0.13-0.24	=
Dense vegetation	0.04	0.10	0.02-0.07	-	0.09	0.10	0.04-0.12	=
Edge	0.09	0.28	0.06-0.13	-	0.22	0.28	0.16-0.28	=

Table 4.5 **Analysis of *Pipistrellus pipistrellus* activity in different microhabitats of Chase Wood, 1996** (χ^2=211.35***)

Micro-habitat	Observed prop. of *P. pip.* passes (n=427)	Expected prop. of *P. pip.* passes	Confidence interval (95%)	Selection
Natural glade	0.39	0.167	0.32-0.45	+
Clear-felled glade	0.07	0.167	0.03-0.10	-
Open woodland	0.23	0.167	0.19-0.30	+
Woodland	0.13	0.167	0.07-0.16	-
Dense vegetation	0.02	0.167	0.00-0.04	-
Edge	0.17	0.167	0.12-0.22	=

4.3.3.1 Selected microhabitats (based on 95% confidence intervals)

Pipistrellus pipistrellus (both phonic types)

1995 (whole season)

- Natural glades
- Ride (with white lights)

1996 (Chase Wood May-July)

- Natural glade
- Open woodland

Myotis spp.

1995 (whole season)

- Natural glades

4.3.3.2 Microhabitats used in proportion to availability (based on 95% confidence intervals)

Pipistrellus pipistrellus (both phonic types)

1995 (whole season)

- Clear-cut

1996 (Chase Wood May-July)

- Edge

Myotis spp.

1995 (whole season)

- One clear-cut (out of two)
- Rides
- Dense vegetation

4.3.3.3 *Avoided microhabitats* (based on 95% confidence intervals)

Pipistrellus pipistrellus (both phonic types)

1995 (whole season)

- Edges
- Dense vegetation
- Ride (unlit)

1996 (Chase Wood May-July)

- Dense vegetation
- Clear-cut
- Open woodland

Myotis spp.

1995 (whole season)

- Edges (three out of four woods)
- One clear felled glade

4.3.3.4 *Microhabitat use by the two pipistrelle phonotypes*

Activity of the two *P. pipistrellus* phonotypes in different microhabitats was compared using 1995 data from Tocil Wood. 55kHz *P. pipistrellus* datasets were not large enough to analyse in the other three study woodlands.

Seventy 55kHz *P. pipistrellus* passes were recorded in Tocil Wood compared with 382 45kHz passes during the same sampling period. Little difference was found in activity between the two types. Both avoided the edge microhabitat, one of the dense woodland categories and both preferred the natural glade. However, the 45kHz type preferred the ride/footpath lit by white

lights while the 55kHz type used this microhabitat in proportion to its availability (see Table 4.6).

Table 4.6 **Microhabitat preferences of 45kHz and 55kHz *Pipistrellus pipistrellus* phonotypes in Tocil Wood, July-Sept. 1995**

	45kHz *P. pipistrellus* χ^2=350.32***				55kHz *P. pipistrellus* χ^2=151.7***			
Micro-habitat	Observed prop. of **45 kHz** passes (n=325)	Expected prop. of **45 kHz** passes	Confidence interval (95%)	Selec.	Observed prop. of **55 kHz** passes (n=54)	Expected proportion of **55 kHz** passes	Confidence interval (95%)	Selec.
Natural glade	0.26	0.06	0.19-0.32	+	0.43	0.06	0.25-0.60	+
Woodland	0.13	0.24	0.08-0.18	-	0.30	0.24	0.13-0.46	=
Ride (lit by white lights)	0.30	0.14	0.23-0.37	+	0.09	0.14	-0.01-0.20	=
Dense vegetation 1	0.11	0.13	0.08-0.16	=	0.04	0.13	-0.03-0.11	-
Dense vegetation 2	0.07	0.13	0.04-0.11	-	0.06	0.13	-0.03-0.14	=
Edge	0.13	0.31	0.08-0.18	-	0.09	0.31	-0.1-0.20	-

In 1996 only 6.79% of the total 427 *P. pipistrellus* passes recorded in Chase Wood were the 55kHz phonotype. As a result of this low sample size, no comparisons could be made between the two types. A similar low quantity of 55kHz *P. pipistrellus* passes was observed in 1995 in Chase Wood where only 28 out of 344 *P. pipistrellus* passes (July-Sept 1995) were recorded as 55kHz.

Lower sample numbers of the 55kHz phonotype may reflect either a lower overall density of this *P. pipistrellus* phonotype in the area, or, an avoidance by the 55kHz type of woodland areas. Vaughan (1996) found that 55kHz pipistrelles mainly used riverine habitats while 45kHz pipistrelles foraged in a variety of habitat types.

4.3.3.5 Changes in microhabitat use during 1995 season (P. pipistrellus)

Some general trends in microhabitat selection or avoidance can be seen from Table 4.7. The same pattern of edge avoidance was apparent in each of the woodlands throughout the 1995 season. Areas of natural glade were preferred sites of activity throughout the season. This concurs with the results (see above) from total pipistrelle passes for the whole 1995 season.

However, changes in preference for or against other microhabitats were apparent during the 1995 season. For example, the two clear felled glades studied (Long Itchington and Chase Wood) were used in proportion to availability until late in the season when they were selected.

Open woodlands were sometimes selected by pipistrelles, particularly during high summer and they were never avoided. Open woodland in Chase Wood was a preferred microhabitat until the end of the season when it was used in proportion to availability. This decline in usage coincided with an increase in activity in the neighbouring clear-cut glade.

Areas with dense vegetation were used in proportion to availability or avoided from mid-season onwards, but early in the year they were used in proportion to availability.

The cycle path lit by white lights in Tocil Wood was a preferred site of activity from mid to late-season. The long straight ride in Long Itchington Wood was avoided during June and July but was used in proportion to availability from August onwards.

No preference or avoidance was shown in early 1995 for any features of Tocil Wood. Bats were evenly distributed throughout.

The results do not provide any obvious support for the hypothesis that habitat preferences are a function of wing loading and that pregnant females may

Table 4.7 **Seasonal changes in microhabitat preferences among *Pipistrellus pipistrellus* during 1995**

Micro habitat	Woodland	**Early season** (late March to late May)			**Mid-season** (early June to mid-July			**Late season** (late July to mid-September		
		+[a]	No pref	-[b]	+	No pref	-	+	No pref	-
Natural glade	Tocil		✓		✓			✓		
	Chase	✓				✓		✓		
Clear-cut glade	Chase		✓			✓		✓		
	Long Itch	Insufficient data				✓		✓		
Open woodland	Rough 1		✓		✓			Insufficient data		
	Rough 2	✓			✓			Insufficient data		
	Chase		✓			✓			✓	
Woodland	Tocil		✓			✓				✓
	Chase	✓			✓				✓	
	Long Itch 1	Insufficient data			✓				✓	
	Long Itch 2	Insufficient data			✓			✓		
Ride	Tocil		✓		✓			✓		
	Long Itch	Insufficient data					✓		✓	
Dense vegetation	Tocil 1		✓				✓		✓	
	Tocil 2		✓			✓				✓
	Rough		✓			✓		Insufficient data		
	Chase		✓				✓		✓	
	Long Itch	Insufficient data					✓			✓
Edge	Tocil		✓				✓			✓
	Rough			✓			✓	Insufficient data		
	Chase			✓			✓			✓
	Long Itch	Insufficient data					✓			✓

move to more open habitats while pregnant (mid-season). However, the bats detected during this study probably constituted a mix of females and males.

[a] + indicates that the microhabitat was selected
[b] - indicates that the microhabitat was avoided

4.3.3.6 Edges

Edges were avoided in this study in 1995. This contradicts earlier work by Walsh and Harris (1996a), and de Jong (1994). However, field work was carried out throughout the night in this study, (in many other studies, field work is carried out for the first hour or two after dusk) and analyses were conducted using nightly bat pass totals. To ensure that the edge avoidance result was not merely a consequence of timing (more bats may be found at the edge earlier in the night, while commuting), Chi-square tests were carried out using the number of bat passes during the first transect walked each night in a woodland. Chi-square tests for each woodland's first transects were significant, indicating that microhabitats were not used in proportion to availability immediately after dusk (where n=total number of bat passes: Tocil (n=140) χ^2=16.9***; Roughknowles (n=33) χ^2=31.9***; Chase (n=181) χ^2=164.9***; Long Itchington (n=100) χ^2=20.9***). In each woodland, except Tocil, edges were avoided microhabitats during the first transect after dusk.

4.3.4 Factors affecting distribution of bats in woodland

Possible reasons for an uneven distribution of flying bats within a woodland include:

- Variations in insect prey availability
- Variations in foliage density affecting flight and echolocation

4.3.4.1 Variations in prey availability

No correlation was found between bat activity in different features (*P. pipistrellus* and *Myotis* spp.) and insect availability in 1995 (sweep net samples from each feature, four nights in June and July) (Figs 4.1 & 4.2).

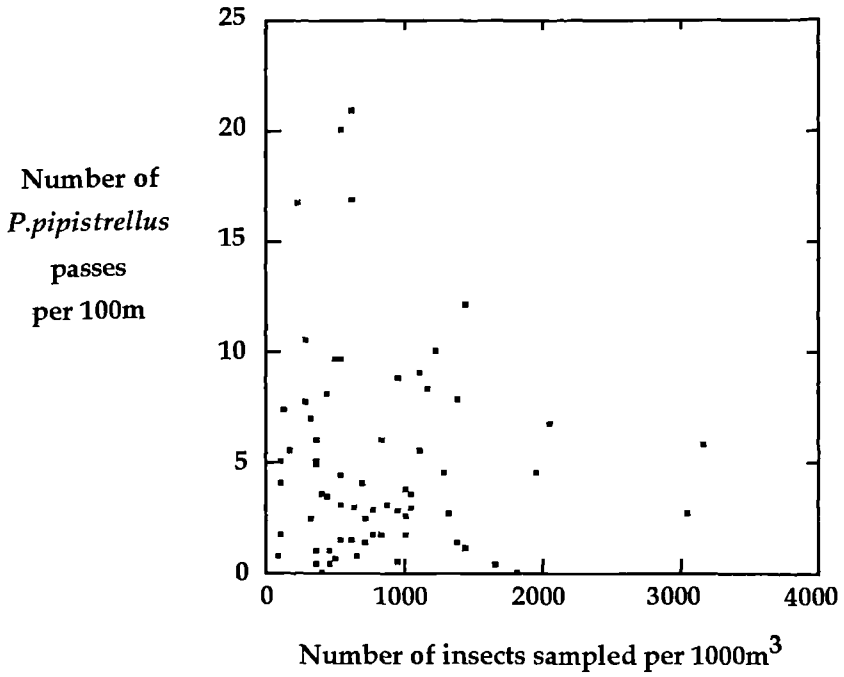


Fig 4.1 Average number of insects caught in sweep net, plotted against *P. pipistrellus*activity in each microhabitat, 1995

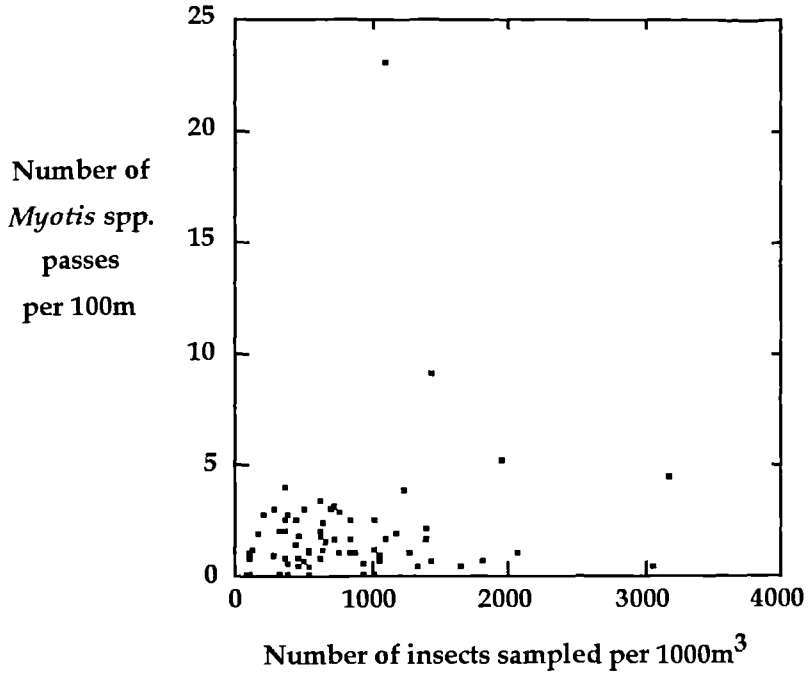


Fig 4.2 Average number of insects caught in sweep net, plotted against *Myotis* spp. activity in each microhabitat.

From linear regression analysis, a significant negative relationship was found between sweep net sample numbers in each microhabitat (in June and July 1995) and the index of vegetation density in canopy and shrub layers (n=87, F=11.82, p<0.01) (Fig 4.3). There was also a similar relationship between netted insects in each microhabitat and cover abundance of the canopy (n=86, F=4.02, p<0.05) (Fig 4.4).

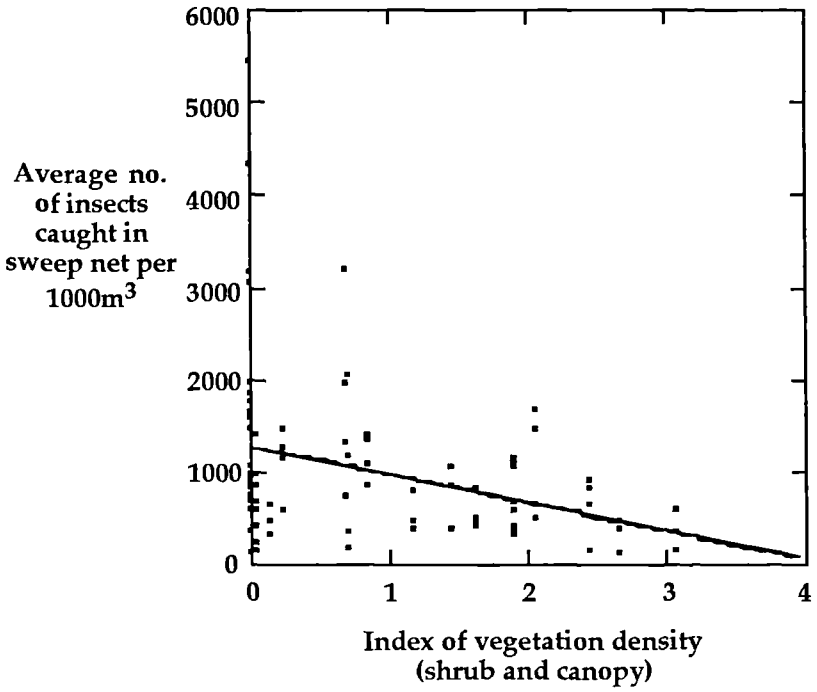


Fig 4.3 Insects caught in sweep net in each microhabitat (June-July 1995) plotted against index of vegetation density of shrub and canopy.
Y=1268.4-307.96X
$F_{(df1, 86)}$=11.82, p<0.01

Comparisons of insect numbers from sweep net catches in this study, in 1995, revealed a significant difference between edges and other microhabitats in one of the woodlands only (Tocil: ANOVA, $F_{(df5,69)}$=2.22, p<0.1; Tukey test, Dense vegetation 2 < Edge, p<0.05). ANOVA's on each of the other woods revealed no significant differences in insect abundance between microhabitats. The negative relationship between sweep-netted insect numbers and vegetation

does not account for the pattern of activity of *P. pipistrellus* or *Myotis* spp. observed in different features.

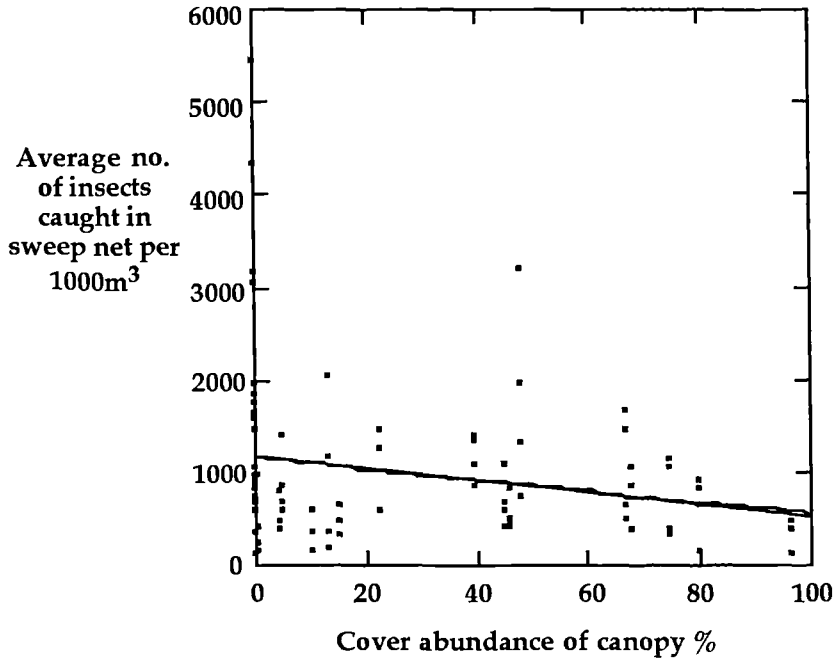


Fig 4.4 Insects caught in sweep net in each microhabitat (June-July 1995) plotted against % cover abundance of canopy.
Y=1146.7-6.1X
$F_{(df1,85)}=4.02$, $p<0.05$

4.3.4.2 Variations in vegetation density/cover abundance

Vegetation density and cover were estimated in July so bat data (per 100m) from June and July were used in analysis (both 1995 and 1996). All four woods (1995) were analysed together (average no. of *P. pipistrellus* passes per feature per night).

Shrub cover abundance showed no discernible relationship with *P. pipistrellus* activity (with DWLS smoothing), either straight line or otherwise.

A correlation was found between the index of density of shrub and canopy layer vegetation combined and *P. pipistrellus* activity. A similar correlation was found between canopy cover abundance and activity. Index of

vegetation density of canopy, average cover of shrub and canopy, and index of vegetation density of shrub layer show similar, though less clear, relationships with activity. For this reason, the index of vegetation density of shrub and canopy layers, and cover abundance of canopy (%), were used in further analyses.

4.3.4.2.1 Nonlinear equations

Linear regression did not describe the relationship between bat activity and vegetation density because at low vegetation densities/cover *P. pipistrellus* activity was low, at high vegetation densities/cover *P. pipistrellus* activity was low, but there was a peak in abundance in between. Nonlinear regression analysis was carried out.

The relationship between *P. pipistrellus* activity and vegetation was found to be linear at first with a rise in abundance associated with small increases in foliage. The relationship then peaks at low levels of vegetation and the tail off is exponential. Several equations produced significant associated F-values ($p<0.05$). A group of three similar equations were found to be the most accurate in representing pipistrelle activity and vegetation data. These were

3. $Y=aX\exp(-bX)$
4. $Y=aX\exp(-bX^c)$
5. $Y=aX^b\exp(-X)$

(see section 4.2.3.2.1)

Another parameter to define the intersect with Y was then entered into each equation. Number 3 was found to consistently produce high F-values for several combinations of pipistrelle density and vegetation density or cover abundance. Table 4.8 shows the different combinations of data analysed and the resulting F-

values using each of the above three equations. Equation 3 was therefore used for further analysis.

Table 4.8 **Using F-values to determine the most accurate equation for describing variations in *P. pipistrellus* activity with vegetation density**

Pipistrelle activity (Y) (June-July)	Vegetation measurement (X)	$Y=a+bX\exp(-cX^d)$ (equation 4)			$Y=a+bX^c\exp(-X)$ (equation 5)			$Y=a+bX\exp(-cX)$ (equation 3)		
		F	DF	r^2	F	DF	r^2	F	DF	r^2
4 Woods 1995	Veg. density[1]	56.25	84	0.48	**62.96**	85	0.41	61.21	85	0.4
	Cover abund. [2]	2.00	83	0.00	32.6	84	0.13	**42.59**	84	0.25
3 Woods 1995	Veg. density	45.93	60	0.51	49.39	61	0.42	**79.47**	61	0.59
(excl. Long It.)	Cover abund.	37.56	59	0.44	21.30	60	0.04	**38.65**	60	0.32
Chase 1995	Veg. density	42.39	20	0.82	21.15	21	0.58	**59.19**	21	0.82
	Cover abund.	3.51	20	0.00	4.91	21	0.00	**43.30**[3]	21	0.76
Chase first	Veg. density	25.44	26	0.67	22.55	27	0.54	**35.44**	27	0.67
transect 1995	Cover abund.	4.03	26	0.00	6.31	27	0.05	**33.07**[4]	27	0.65
Chase 1996	Veg. density	14.57	32	0.33	20.26	33	0.34	**20.40**	33	0.34
	Cover abund.	19.74	28	0.48	15.48	29	0.26	**22.18**	29	0.42
Chase without	Veg. density	6.58	21	0.2	4.41	22	0.22	**9.02**	22	0.19
full moon1996	Cover abund.	9.36	21	0.35	8.75	22	0.18	**10.67**	22	0.26

[1] Veg. density refers to the combined index of vegetation density of shrub and canopy layers, see section 4.2.2
[2] Cover. abund. refers to percentage cover abundance of the canopy layer.
[3] Although the F value is highly significant here, the resulting line is very steep and rises above logical Y values. This graph is therefore not used.
[4] Same as 3.

4.3.4.2.2 Using equation 3 as a model

$$Y = a + bX\exp(-cX)$$

This line intersects the Y axis at a point > 0 and shows a linear rise in pipistrelle passes with vegetation density. A point of inflection then occurs at an optimum vegetation density or cover and the tail-off is exponential, although the line never reaches zero[1] .

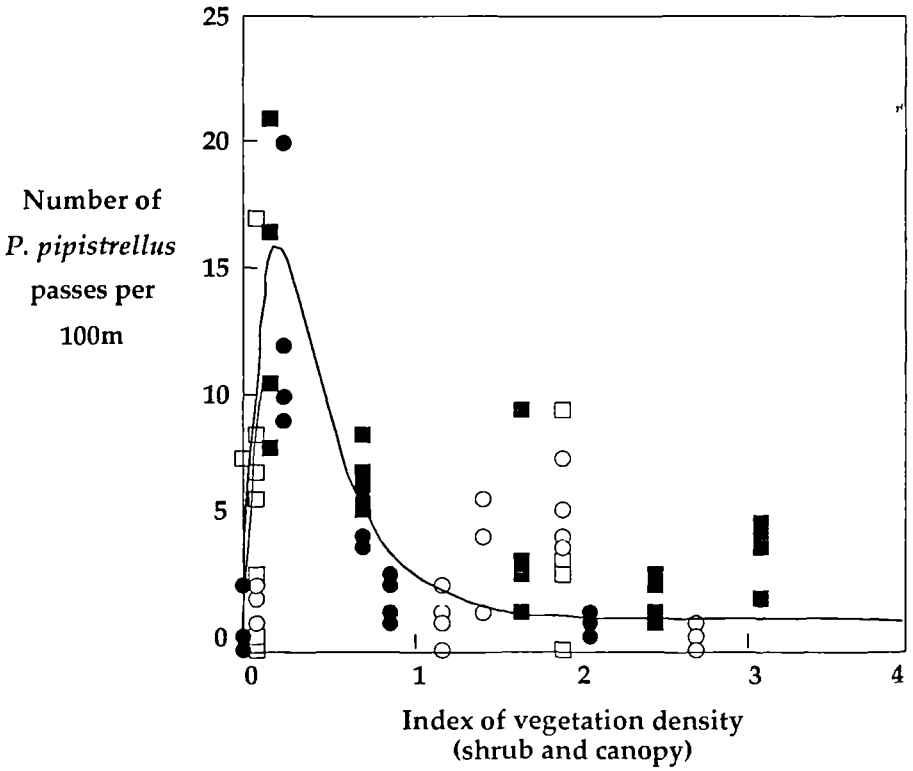


Fig 4.5 The relationship between *P. pipistrellus* activity and vegetation density in broadleaved woodland (June-July 1995) where; ○ = Long Itchington Wood, ■ = Chase Wood, ● = Tocil Wood and □ = Roughknowles Wood.

Equation of the line shown is
$Y = 1.43 + 181.56X\exp(-4.6X)$
$F_{(df3,85)} = 61.21$, $p < 0.01$

[1] In the field, few bats were observed in very densely vegetated microhabitats. However, a line intersecting the X axis (X=0 at some point along the line) may be inaccurate. Although bats cannot fly in shrub or canopy where, hypothetically, 100% of space is take up by vegetation, it is possible for them to travel past above the canopy layer.

Figs 4.5 and 4.6 show *P. pipistrellus* activity from all four woodlands plotted against vegetation density from shrub and canopy layers, and cover abundance of the canopy (%), respectively.

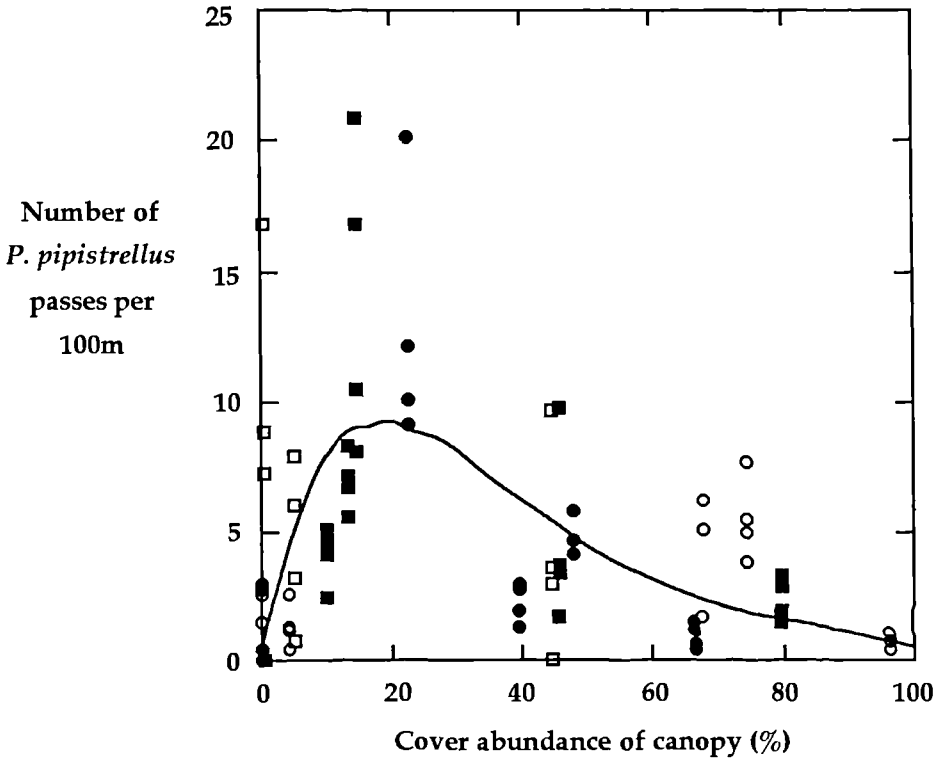


Fig 4.6 The relationship between *P. pipistrellus* activity and cover abundance of canopy vegetation in broadleaved woodland (June-July 1995) where; o= Long Itchington Wood, ■= Chase Wood, ●= Tocil Wood and □= Roughknowles Wood.

Equation of the line shown is

$Y=0.1+1.28X\exp(-0.05X)$

$F_{(df3,84)}= 42.59$, $p<0.01$

Edge microhabitat data was omitted from graphs in order to prevent clogging of the Y axis, although it was included in analyses. Plots with cover abundance (Fig 4.6) are generally broader than those with vegetation density (Fig 4.5).

In Long Itchington Wood, *P. pipistrellus* activity was greatest at higher vegetation densities compared to the other three study sites (Fig 4.5 & Fig 4.6).

Removal of Long Itchington data from the model results in a higher F-value with vegetation density (Fig 4.7) but a lower F-value with cover abundance of canopy (Fig 4.8). This suggests that inclusion of Long Itchington data in the model makes little difference to the fit of lines.

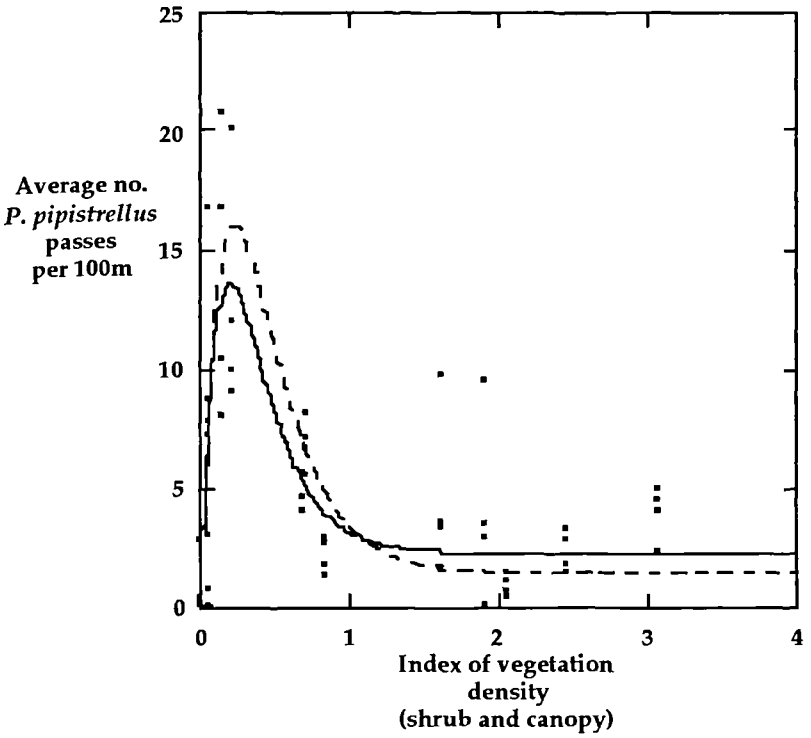


Fig 4.7 *Pipistrellus pipistrellus* activity in three woods, excluding Long Itchington, plotted against index of vegetation density. The dotted line shows the line of best fit with Long Itchington data included in the analysis (as in Fig 4.5) and the unbroken line shows the fit without Long Itchington data.

Equation of the unbroken line is
$Y=2.27+163.62X\exp(-5.33X)$
$F_{(df3,61)}=79.47$, $p<0.01$

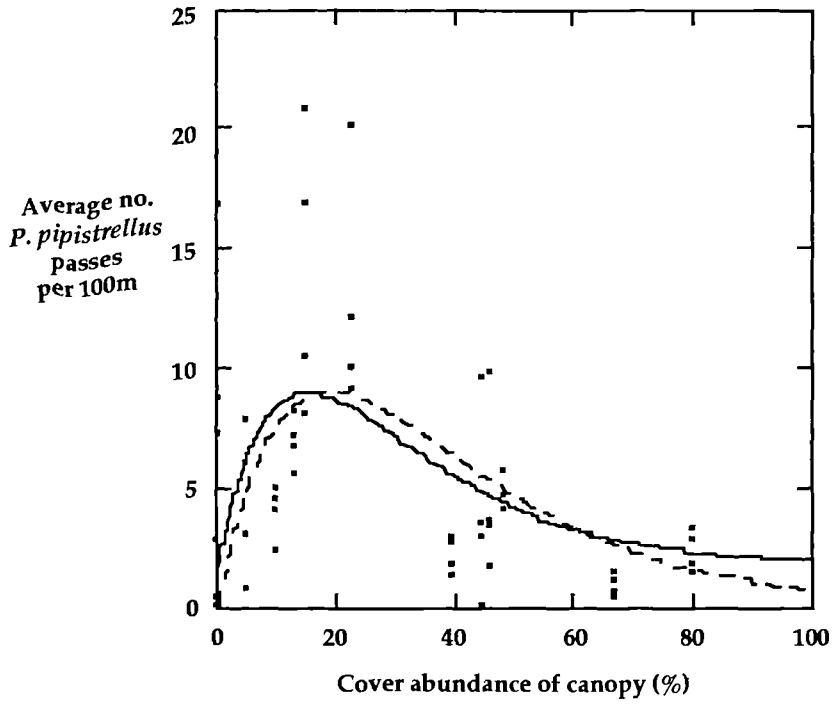


Fig 4.8 *P. pipistrellus* activity in three woods, excluding Long Itchington, plotted against cover abundance of canopy. The dotted line shows the line of best fit with Long Itchington data included in the analysis (as in Fig 4.6) and the unbroken line shows the fit without Long Itchington data.

Equation of the unbroken line is
$Y=1.76+1.29X\exp(-0.07X)$
$F_{(df3,60)}=38.65$, $p<0.01$

Myotis spp. activity was much lower than *P. pipistrellus* so regression analysis could not be carried out accurately. However, graphically presented 1995 data shows a similar peak in numbers at low vegetation densities such as those found in natural glades (Figs 4.9 & 4.10).

P. pipistrellus activity patterns in 1996 were similar those in 1995. 1996 data (from Chase Wood only) plotted against the index of vegetation density is shown in Fig 4.11 along with data from the first transect covered during the night in Chase Wood, June and July 1995. First transect data from Chase Wood (1995) is shown in these graphs because in 1996 surveying was done during the first two hours following sunset.

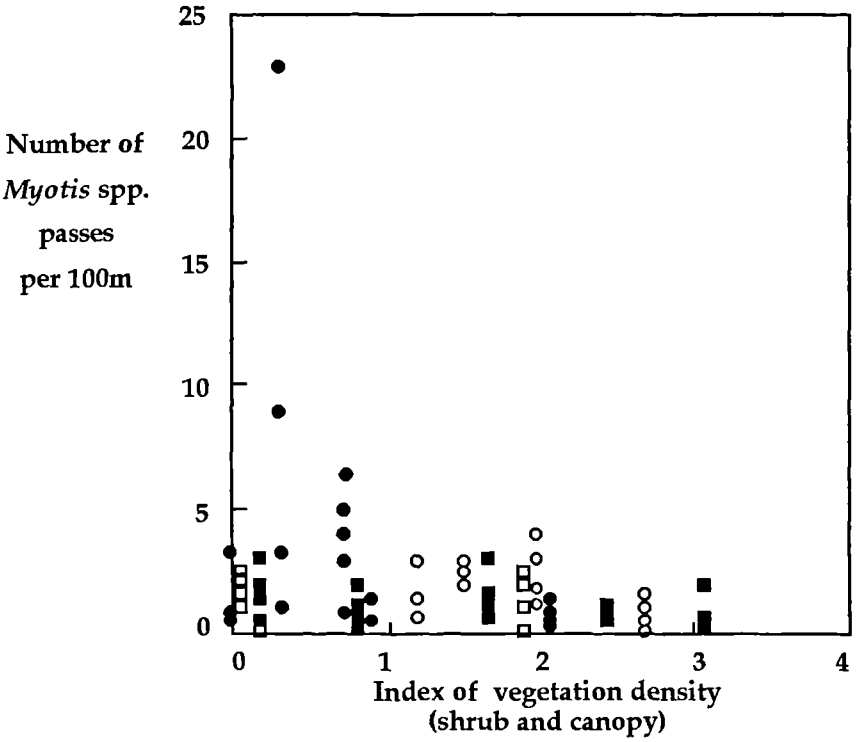


Fig 4.9 *Myotis* spp. activity and vegetation density in broadleaved woodland (June-July 1995)

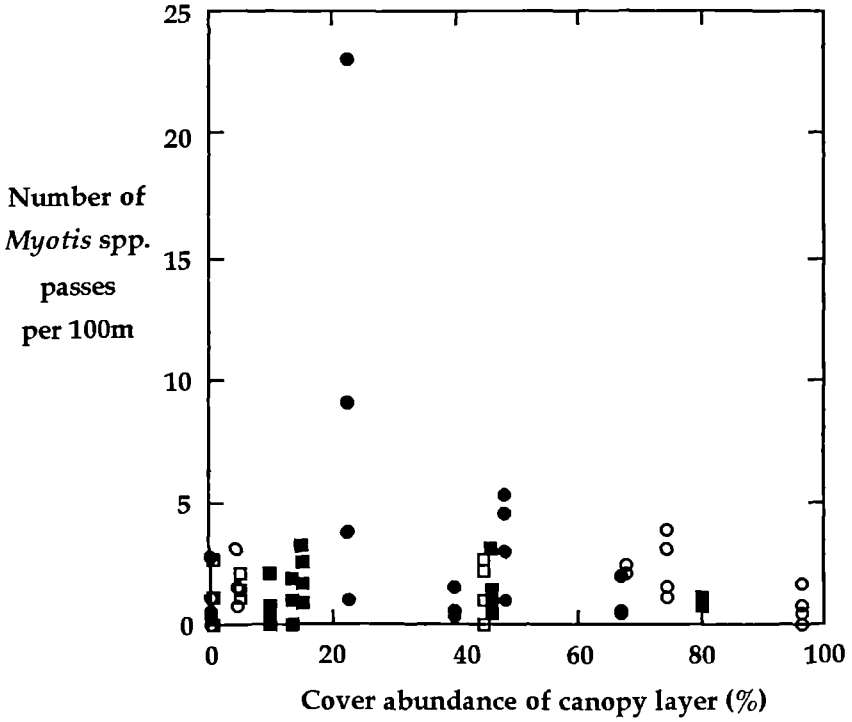


Fig 4.10 *Myotis* spp. activity and cover abundance of canopy vegetation in broadleaved woodland (June-July 1995).

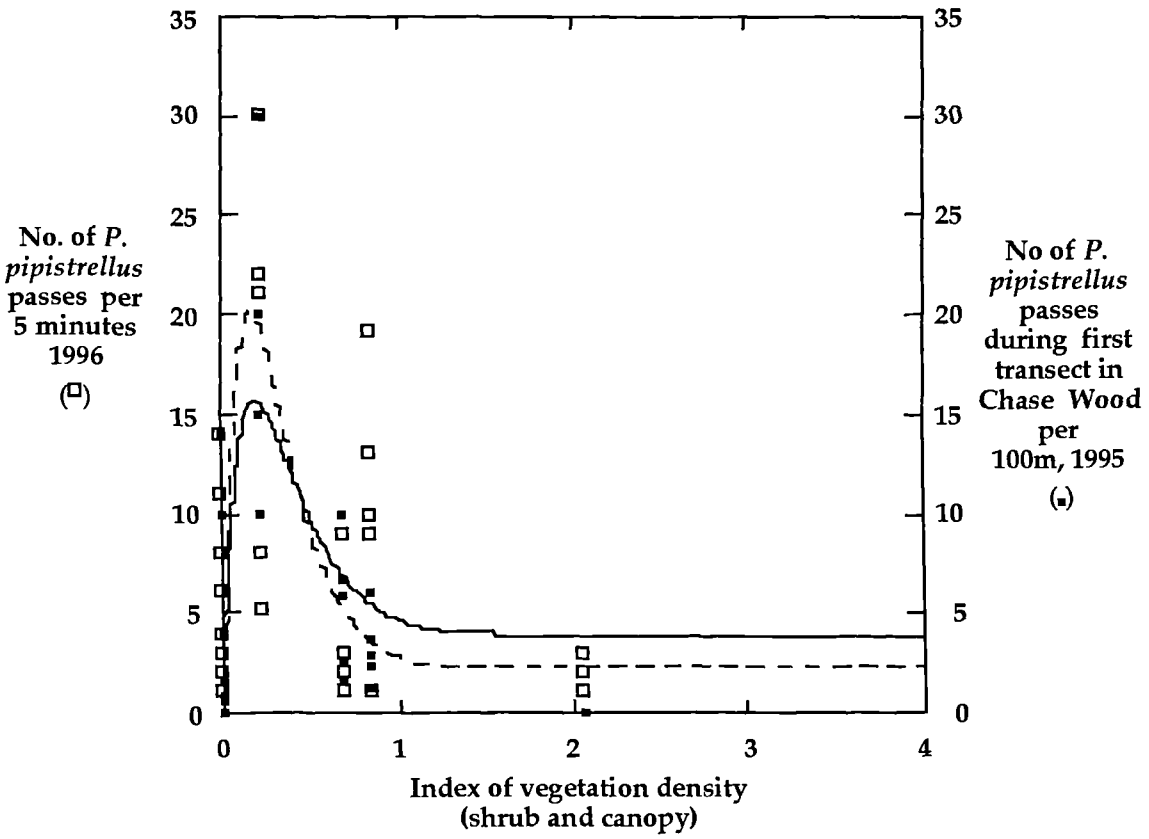


Fig 4.11 *P. pipistrellus* activity and the index of shrub and canopy density during 1996 (——), Chase Wood, and the first transect covered in Chase Wood, 1995 (- - -).

Equation of the unbroken (1996) line is
$Y=3.96+174.92X\exp(-5.47X)$
$F_{(df3,33)}=20.4$, $p<0.001$

Equation of the dashed (1995) line is
$Y=2.29+306.72X\exp(-6.3X)$
$F_{(df3,27)}=35.44$, $p<0.001$

Data in 1996 was collected irrespective of stage of lunar cycle. In order to determine whether this has had an effect on bat activity, nights of data collection around the full moon were removed from analysis and only those from days 6 to 15 of the lunar cycle (mid to new moon) were included. Fig 4.12 shows activity, excluding nights of full or near-full moon, plotted against vegetation density. This graph shows a lower peak than Fig 4.11 where these data were not removed.

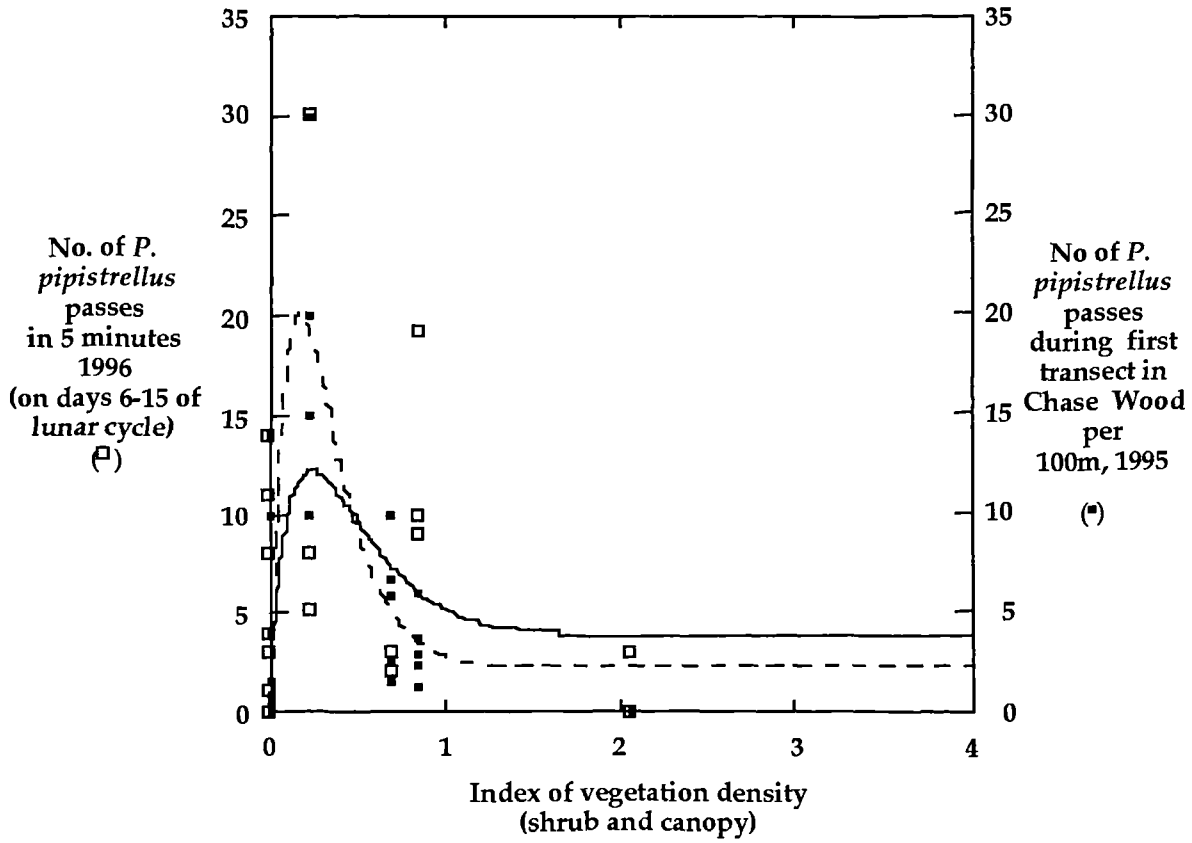


Fig 4.12 *P. pipistrellus* activity and vegetation density of shrub and canopy layers in Chase Wood, 1996 (——) on nights of new-half moon, and during the first transect walked in Chase Wood, 1995 (- - -).

Equation of the unbroken (1996) line is
$Y=3.89+98.86X\exp(-4.33X)$
$F_{(df3,22)}=9.02$, $p<0.001$

Equation of the dashed (1995) line is
$Y=2.23+306.72X\exp(-6.3X)$
$F_{(df3,27)}=35.44$, $p<0.001$

When activity from 1995 and 1996 are compared, it appears that 1996 data are more diffuse with lower peaks and higher Y intersections. Direct comparisons cannot be made because methods of data collection were different in both years (however, see section 7.3.6). It can be seen that the peak in activity in 1995 is more defined than in 1996. In 1996, the edge feature of Chase Wood was not avoided as in the previous year.

Chase Wood 1996 data plotted against cover abundance of canopy, is shown in Fig 4.13.

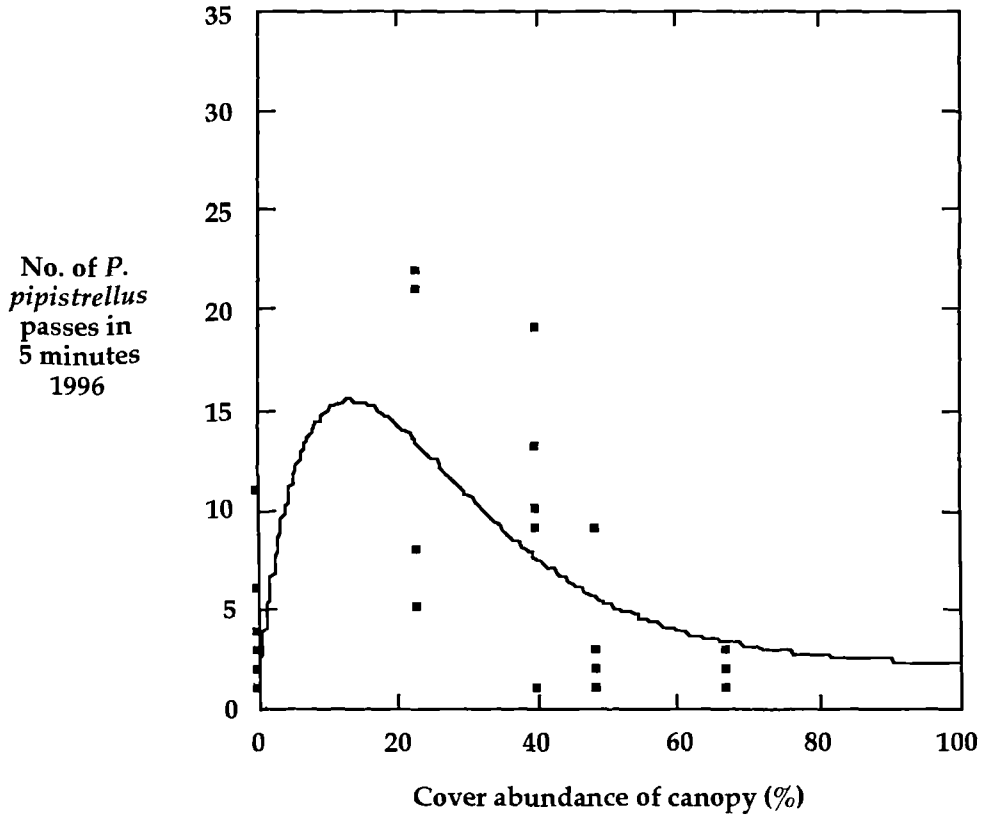


Fig 4.13 Activity of *P. pipistrellus* in Chase Wood (1996) with cover abundance of canopy

Equation of the line shown is
$Y=2.22+2.74X\exp(-0.08X)$
$F_{(df3,29)}=22.18$, $p<0.01$

4.4 Discussion

4.4.1 Microhabitat selection

Natural glades were preferred microhabitats for both *P. pipistrellus* and *Myotis* spp. throughout 1995 and 1996. This concurs with the findings of Walsh and Harris (1996a) and de Jong (1994). The two clear-cut microhabitats which were studied in Chase and Long Itchington Woods were selected by pipistrelles from August to September. If, as Walsh and Harris (1996a) suggest, high activity

of bats at clear-cuts merely reflects a preference for edge type habitats then a corresponding increase in edge activity could be expected during the late part of the season. However, this was not the case.

Comparisons were made of overall activity between woods and no significant differences were found. However, there were differences in relative activity in selected microhabitats. Two of the study sites represented extremes in the vegetation density spectrum: Roughknowles Wood which had been thinned recently and replanted, and Long Itchington which has dense vegetation.

Roughknowles had significantly lower *P. pipistrellus* activity in microhabitats for which a preference was shown, compared with preferred microhabitats of two of the other study sites, Chase and Tocil. This is unsurprising given the lack of shelter in the wood.

Less *P. pipistrellus* activity was observed in preferred microhabitats of Long Itchington compared with selected microhabitats along transects in both Chase and Tocil. Long Itchington is intensively managed and large areas are covered in dense growth of young trees or coppice. This results in a concentration of bats in mature tree stands (standards with some coppicing) within the wood. Natural glades in Long Itchington Wood are uncommon and bats utilise areas with higher densities of vegetation than in other woods.

4.4.2 Edge avoidance

Both Walsh and Harris (1996a) and de Jong (1994) noted that clear-felled areas or open areas within woodlands and edges were selected by some species of bat. However, in this study edges were usually avoided, particularly in 1995. This apparent contradiction may be explained by comparisons being made. Walsh and Harris (1996a) compared woodland edges with a wide variety of habitats including arable land and rivers. However, de Jong (1994) concentrated

on woodland microhabitats and found that edges between forests and open areas were selected by some species. In this study, edges were compared with other woodland microhabitats and the result, edge avoidance, would seem to contrast with the findings of de Jong (1994). Vaughan (1996), on the other hand, compared bat activity within woodlands with activity at edges and found no significant difference between the two.

De Jong found an overall preference by *P. pipistrellus* for edges. However, when edges were separated into various types, such as fields bordered by coniferous woodland, or grassland verging with wet woodland, the only edge microhabitat for which *P. pipistrellus* showed a preference was the edge of grassland and deciduous woodland. All other edge types were used in proportion to their availability. In the present study only one edge bordered grassland, but this was also avoided. Edges were avoided by *M. mystacinus* in de Jong's study (1994).

It has been hypothesised that insects accumulate in re-circulating air to the leeward of windflow (e.g. Lewis, 1970; Lewis and Dibley, 1970). However, similar work by Bowden and Dean (1977) and Dean (1974) on the distribution of insects in and near a tall hedgerow led to a contradictory hypothesis that the pattern and distribution of aerial insects appeared to be determined mainly by comparative richness of vegetation irrespective of wind speed or direction. Peng (1991) reviewed evidence from his study of dipteran flies around emergent trees and deduced that wind was a major factor affecting abundance of aerial insects but that insect diversity may be determined by vegetation.

The aspect of an edge may influence the abundance of insects, depending on wind direction, and may therefore be a factor influencing its selection or avoidance by bats. Edges in this study in each woodland were facing different

directions (see section 2.2). They also bordered different habitats: arable land, a meadow nature reserve and roads.

High insect availability at edges is proposed as one of the reasons for the edge selection noted by Walsh and Harris (1996a) and de Jong (1994) along with the suitability of these areas for flight free of clutter (Walsh & Harris, 1996a). The insect abundance hypothesis was confirmed by de Jong (1994) who compared insect abundance ($mg/100m^3$) within forests, at forest edges and in open areas. He found high densities in open areas and a decline in availability from open areas to edges to woodland. Comparisons of insect numbers from sweep net catches, in 1995, revealed a significant difference between edges and one other microhabitat (Dense vegetation 2) in Tocil Wood. No significant difference in insect abundance between different features were found in each of the other woodlands. However, a plot of sweep net sample numbers against vegetation density or cover abundance of microhabitats shows a negative relationship between the two (Fig 4.3 & 4.4). This decline in insect numbers from open to cluttered microhabitats concurs with de Jong's findings and contrasts with the findings of Kalcounis and Brigham (1995) that insect availability is greater in cluttered areas.

Edge avoidance in 1995 by both *P. pipistrellus* and *Myotis* spp. was almost consistent throughout the four woodlands and, for pipistrelles, throughout the season, despite differing aspects and borders of edge microhabitats. This suggests that there were reasons other than insect availability or sheltering from wind which affected bats' preferences.

Many species of bat are known to fly along linear landscape elements and edge features when commuting to and from roosts. This may be a mechanism protecting against aerial predation (Limpens & Kapteyn, 1991). It is possible that

bats flying at woodland edges are at a greater risk from predation than bats flying within woods. Foraging in edge habitats may only be worthwhile when prey is much more abundant there to offset the increased risk of predation. There was no significant difference in sweep net sample numbers between most of the microhabitats studied and bats in 1995 were more active within the humid (Neal, 1958) and sheltered woodland environment.

It is possible that the edge selection found in other studies may have been a result of field work timing. If field work is carried out immediately after sundown then high levels of activity at edges may be due to the presence of commuting bats (see section 1.4.1.1). However, in this study edge avoidance was noted during the early part of the evening in three out of the four study woodlands.

Some authors have suggested that relative humidity has an important effect on flight activity (Watkins, 1972; Lacki, 1984; Adam *et al.*, 1994). The summer of 1995 was the hottest and driest summer in the study area since records began (1893 & 1870 respectively). Average daytime (23.3°C) and night-time (12.4°C) temperatures were the highest on record, with daytime temperatures 3.1°C above normal (BWS). Hot dry weather in 1995 may have resulted in bats using small natural glades to a greater extent than more open edges and clear-cut areas compared with other studies where edges and clear-cuts have been preferred. More detailed analysis of weather data and bat activity can be found in Chapter 6.

In 1996, edges were used by *P. pipistrellus* in proportion to their availability according to results from the adapted Chi-square test. This could reflect a reduction in the importance of internal woodland features as foraging

sites given the higher rainfall and lower temperatures of the summer of 1996 (see section 6.4.9).

4.4.3 Dense vegetation avoidance

P. pipistrellus was found to avoid dense vegetation, particularly from mid to late season. This confirms an earlier study (de Jong, 1994) and has practical implications for woodland management. Coppicing in a wood can increase invertebrate diversity (Kirby, 1992). However, results from this study suggest that bats, particularly *P. pipistrellus,* do not use mature coppice areas in proportion to their availability preferring, instead, more open glades. *P. pipistrellus*, did however, use dense vegetation in proportion to its availability early in 1995. Development of leaves in the canopy may restrict access to pipistrelles from June onwards.

Long Itchington is a protected Site of Special Scientific Interest and has been described as one of the best remaining examples of coppice-with-standards woodlands still traditionally managed in the English Midlands (WBRC). However, the practice of intensive coppicing is unlikely to benefit *P. pipistrellus* observed in this study. It is a relatively fast flying species with loud echolocation and is not adapted for flight in cluttered spaces (Baagöe, 1987).

Dense vegetation was not avoided by *Myotis* spp. in this study. The diet of *M. mystacinus* (whiskered bat) has been found to contain some flightless entemofauna which suggests that a small proportion of its prey is taken by gleaning (Hollyfield, 1993). Thus, the whiskered bat may be better adapted to flying in clutter than the pipistrelle.

4.4.4 A model describing microhabitat use by P. pipistrellus

The equation best describing *P. pipistrellus* activity in different woodland features in 1995 and 1996 is a nonlinear one (see equation 3). This equation describes a line with a maximum (peak) along with a single inflection point. The first parameter, *a*, determines the intersect with the Y axis. The second describes the slope of the first segment of the line, with higher values resulting in a steeper gradient. This is demonstrated in Figs 4.5 & 4.6.

Graphs with cover abundance, by comparison with vegetation density, show less distinctive peaks with more rounded curves. Figures 4.5 and 4.6 show *P. pipistrellus* activity plotted against index of vegetation density and against cover abundance of canopy. Cover abundance graphs peak at lower activity levels than vegetation density graphs. The nature of the relationship is the same with both because there is an initial linear increase, then a peak followed by an exponential tail-off. Cover abundance is easily estimated and results in a more dispersed graph and easily visible changes in activity with vegetation.

All of the graphs (Figs 4.5 - 4.13) show an initial increase in bat activity, indicating a preference for the shelter of woodland over exposed edges or clear-cuts.

The peak of the graphs suggest that there is an optimum vegetation density or cover which allows unhindered flight and echolocation while providing the shelter, humidity and high insect abundance characteristic of woodlands. The position of this peak may be dependent upon weather conditions. It is possible that during a wet and cool summer the peak will move closer to the Y axis indicating greater bat activity in more open areas, or, that in a wetter or cooler summer the peak will be less defined, indicating a more even distribution of bat activity.

1996 was wetter and cooler than 1995 (see section 6.4.9) and graphical comparisons of data from the two years (Fig 4.11 & 4.12) show a more even spread of *P. pipistrellus* activity in 1996. Edges were not avoided in 1996 by *P. pipistrellus* compared with 1995. The limited data available appear to show some changes in activity preferences during the two years.

There is an exponential decline in relative bat activity with increasing foliage abundance. This reduction in activity was evident in 1995 and 1996. Increased vegetation density reduces the ease with which bats can fly, echolocate and hunt, particularly in the case of the most commonly observed bats in this study, *P. pipistrellus*.

1996 data excluding nights with a full moon show a slightly lower activity peak than data including all stages of the lunar cycle. This may indicate that pipistrelles are more active in the woodland during bright stages of the lunar cycle, but because of the low number of nights involved, this conclusion is tenuous.

4.4.5 Summary

The results of the two main analyses carried out in this Chapter, Chi-square testing and nonlinear regression, correspond. Very open microhabitats were avoided along with densely vegetated areas and intermediate microhabitats with low levels of vegetation were preferred. This finding contrasts with insect availability in and around a woodland and suggests that distribution and relative activity of bats within woodland microhabitats is affected more by their echolocation and flight abilities than the relative abundance of insects.

Chapter 5

INSECT DIVERSITY, BAT DIET AND NOCTURNAL ACTIVITY PATTERNS

5.1 Introduction

This chapter examines relationships between prey diversity and bat activity in 1995. Little is known of the invertebrate fauna available to bats in deciduous woodlands. The range of invertebrate taxa are examined, particularly with reference to peaks in *P. pipistrellus* activity and previous work on diet of this species.

Also, nocturnal pipistrelle activity is related to previous work on activity from roost counts and graphically compared with insect availability from the suction trap during the night.

5.1.1 Diet and prey availability

Relationships between bat diet and prey availability vary from species to species. Brigham and Saunders (1990), for example, examined the diet of *Eptesicus fuscus* (the big brown bat) in Canada in relation to the available prey. They concluded that the diet of this species was probably selective but could vary with the size and type of prey available. Diet was dominated by coleopterans, despite the fact that only 1.9% of insects captured in various traps belonged to this order. They found no significant correlation between insect availability and diet.

Also in Canada, a correlation was found between prey availability and diet of *M. lucifugus* (Belwood and Fenton, 1976). Chironomid flies constituted at least 30% of the diet. Adult males' diets were composed of insects roughly in proportion to their abundance in a malaise trap. Lactating females, however, took larger numbers of Trichoptera and Lepidoptera (Belwood and Fenton, 1976).

Hollyfield (1993) found that the diet of *M. mystacinus* was comprised, from May to August, of over 49% Diptera and nearly 35% Lepidoptera. Arachnida and

Coleoptera were the next most important prey groups at 5.64% and 3.85% respectively. Diptera composed 92.58% of insects caught in a suction trap and Arachnida and Coleoptera composed less than 1% combined. Therefore, Diptera were negatively selected, while Arachnida and Lepidoptera were positively selected, suggesting that the diet of *M. mystacinus* is not entirely opportunistic.

Prey selection is difficult to quantify, however, because the prey available to a bat may not necessarily be reflected in any insect trap catches. For example *N. noctula* flies at heights of up to 30m (Corbet and Harris, 1991) and few, if any, insect studies have trapped at that height. Also, the prey available to a bat are largely a function of its morphological and echolocatory characteristics (Norberg and Rayner, 1987) and trap catches will not necessarily mirror this.

5.1.1.1 Pipistrellus pipistrellus diet

Diet of *P. pipistrellus* has been examined by several authors (Barlow, 1997; Sullivan *et al.*, 1993; Swift *et al.*, 1985). In Scotland, Swift *et al.* (1985) examined prey abundance using a Johnson-Taylor insect suction trap in areas where bats foraged intensively. They found that the diet of bats caught in the study area generally reflected the abundance of insects available to them, for example Chironomidae constituted 53.8% of individuals caught in the trap, whilst this family constituted 56.4% of individuals identified in bat droppings. Neuroptera were present in very small numbers in trap samples (up to 0.3%) but they were present in faeces up to 3.2%, suggesting that they may have been selected.

Sullivan *et al.* (1993) and Barlow (1997) did not trap insects to compare with pipistrelle diet so it is not known if prey types reflected those available. However, Barlow (1997) found that the diets of the 45kHz and 55kHz phonotypes varied, perhaps as a result of the differential habitat use among the two types, as noted by Vaughan (1996).

5.1.2 Nocturnal activity patterns

Swift (1980) examined nocturnal activity patterns of *P. pipistrellus* in Scotland. During pregnancy, patterns consisted of a foraging peak after dusk followed by a gradual decline in activity outside the roost as bats returned between midnight and dawn. After parturition, activity became bimodal with a post dusk and pre-dawn peak as bats returned to and left the roost at irregular intervals during the night. After weaning, the bimodal pattern abated as the adults left the roost and a unimodal pattern of activity with a peak at dusk occurred.

Maier (1992), in a similar study of pipistrelles in Oxfordshire found a unimodal pattern early in the season with a peak after dusk. From mid- to late-May bats remained outside the roost for the whole night (except during cold weather when they returned soon after dusk). From parturition (mid-/late-June) a bimodal activity pattern became obvious until around the time of weaning (late-July) when the pattern became unimodal again.

It is hypothesised that activity patterns of pipistrelles in Warwickshire may follow a similar pattern to those in the neighbouring county of Oxfordshire and may be influenced by availability of insects.

Note: Although some traps caught arachnids and other non-Insecta invertebrates, the term insect is used in this Chapter for simplicity.

5.2 Methods

5.2.1 Bats and insects

Bat activity and insect abundance estimation (in 1995) is described in Chapter 2.

5.2.2 Insect identification

Trap and net catches were identified under a x20/x40 stereo microscope using a variety of identification keys and reference books. These were: Burton (1968), Chinery (1977), Coe, Freeman and Mattingly (1950), Colyer and Hammond (1968), Fraser (1959), Jones-Walters (1989), Roberts (1985 a&b), Sankey and Savory (1974), South (1971 a&b), Tilling (1987), Unwin (1981; 1984) and Wright (1990).

5.2.3 Simpson's diversity index (of available insects)

In order to quantify the diversity of insects found in each site, data were applied to a diversity index. A non-parametric index was required which makes no assumptions about the distribution of the species (families)/numbers. However, the correct index should not only consider the number of families but also abundance.

The Shannon and α (log series) are commonly used indices. The log series is a robust index. However, it is determined using species richness (R) and the number of individuals (N), and where changes in evenness occur and N and R remain constant, no changes are recognised (Hollyfield, 1993). The Shannon index expresses the relative evenness of the abundances of all species. For this reason the Shannon (or Shannon-Weaver equation) has been criticised as an "insensitive measure of the character of species abundance" (May, 1975).

Simpson's index (Simpson, 1949), is a description of the dominance of, or concentration of, abundance into one or two of the commonest species of the community (Poole, 1974). Simpson's index has also been described as a measure of the probability that the second individual taken from a population will be the same species as the first (Pielou, 1975).

Simpson's index was considered the most appropriate for use in this study because a measure of the degree of dominance of a few species in the community rather than the overall evenness of the abundances of species was required. The diversity index would then be more useful in terms of describing insects available to foraging bats. Also, Simpson's index has been used in several bat diet studies (e.g. Barlow, 1997; Hollyfield, 1993; Swift *et al.*, 1985). It is defined as:

$$D = \sum_{i=1}^{n} p_i^2$$

where p_i = the proportion of individuals in the *i*th species. D was divided by 1, so a higher D indicates greater diversity.

This index is strongly influenced by the underlying distribution in that it is weighted towards the most abundant species, not towards species richness (Magurran, 1988).

5.3 Results

5.3.1 Insect availability

Highest catch abundance in the light trap occurred in August in three out of the four woods. In Roughknowles the peak in numbers occurred in late July (30/7). In the suction trap, peaks occurred in July in three of the study

(22/6). Sweep net sample numbers peaked in June in three woods, in Tocil, numbers peaked in the sweep net in early July (1/7) (Figs 5.1-5.3).

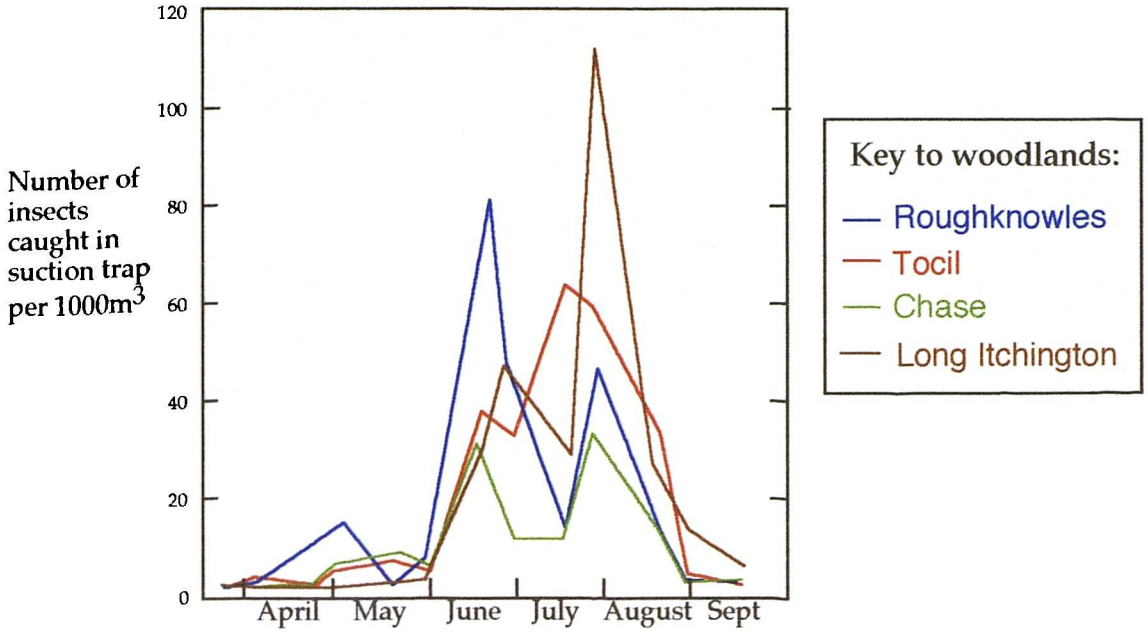


Fig 5.1 Suction trap catches in each woodland during 1995

5.3.2 *Insect taxa present*

14,436 invertebrate specimens were caught in the three traps from March to September, 1995. Of these, 6261 were caught in the light trap, 4787 in the suction trap, and 3388 in the sweep net. All three trap samples had different proportions of arthropod families represented (Table 5.1). The percentages of each invertebrate order caught nightly in traps are illustrated in Appendix I.

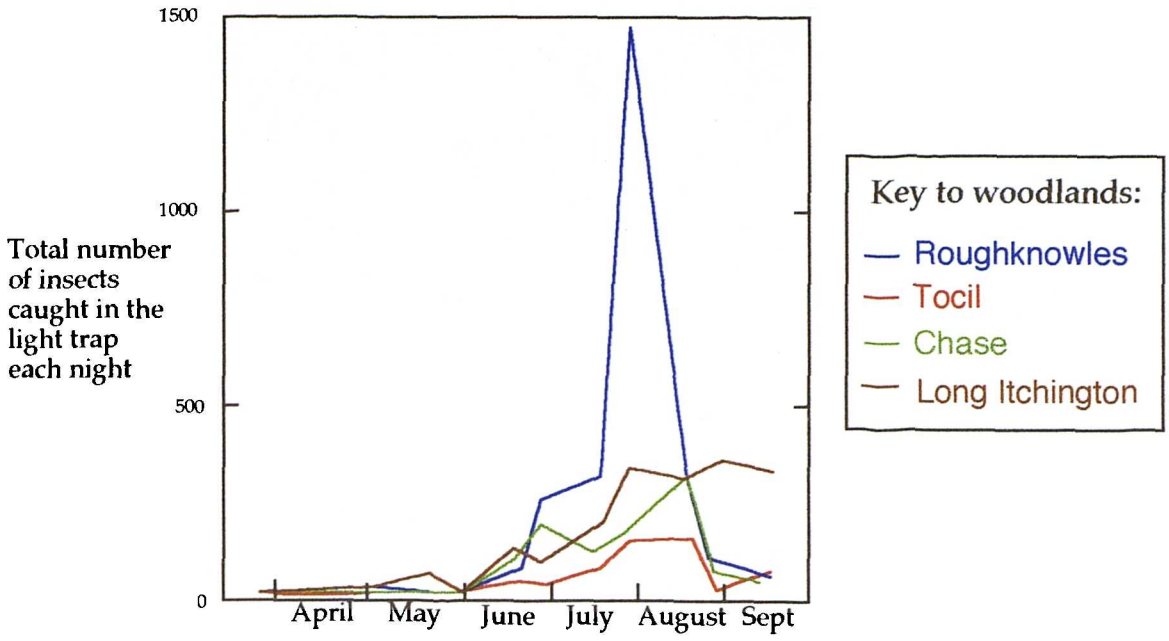


Fig 5.2 Light trap catches in each woodland during 1995

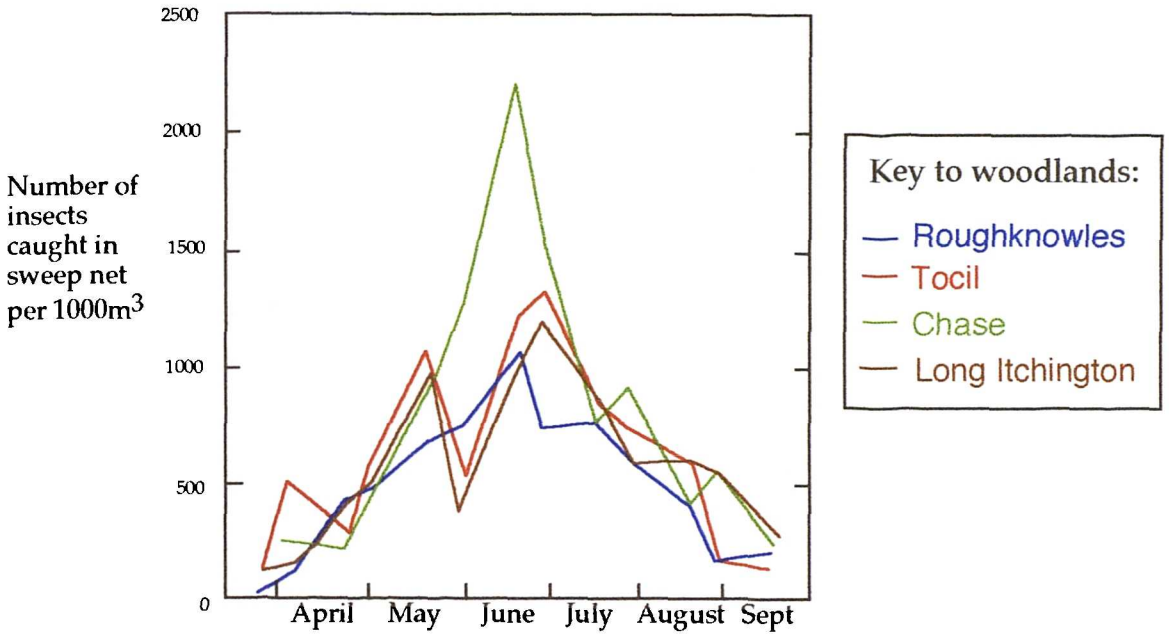


Fig 5.3 Sweep net catches in each woodland during 1995

Table 5.1 **Invertebrate taxa captured using three different trapping methods (percent of total catch), March-September, 1995**

Invertebrate taxon	Suction trap (%) n=4878	Light trap (%) n=6261	Sweep net (%) n=3388
Arachnida	0.2	0.5	11.6
Coleoptera	1.0	3.8	13.8
Diptera	84.7	28.9	23.0
Hemiptera	3.3	12.0	26.8
Hymenoptera	3.6	9.6	8.8
Lepidoptera	4.4	40.5	2.3

Total sample sizes varied between woods, despite a similar number of hours spent trapping in each (Table 5.2).

Table 5.2 **Total number of invertebrates caught in each trap, in each woodland**

Woodland	Suction trap (total no. captured)	Light trap (total no. captured)	Sweep net (total no. captured)
Tocil	1402	666	1183
Roughknowles	1285	2587	499
Chase	619	1123	1110
Long Itchington	1481	1875	596
Σ	4787	6261	3388

An ANOVA carried out on suction trap numbers per $1000m^3$ in each wood (12/13 nights) showed that the difference in numbers was not significant (n=49, F-ratio=0.72, p>0.1). The suction trap operated at a distance of 3m from the ground in all four woodlands and the variable most likely to affect efficiency was windspeed (Southwood, 1978). However, in Roughknowles, the

woodland most prone to windy conditions, the number caught was higher than in Chase Wood. The sampling glade in Chase is more sheltered. Despite a lack of significance in the difference between numbers it is clear that in the height of summer the number of insects caught in Chase Wood was much lower than in the other woodlands (Fig 5.1).

Total captures in the light trap in different woodlands also varied (Fig 5.2, Table 5.2). Catchment area of the light trap probably differed between woods. In Chase and Tocil Woods, the light trap was situated in glades covered by dense bracken from June until September. At the Roughknowles Wood site field layer vegetation consisted of low grasses and small clumps of bramble and did not reduce the catchment area to the same extent as in Chase and Tocil. In Long Itchington Wood, the glade area was covered by very tall grass species, reaching a height of up to 2m around July and August. These grasses probably allowed a greater amount of light through than the bracken covered glades, nonetheless, the catchment here would have been smaller than in Roughknowles Wood. However, no significant difference was found in numbers of insects caught in the light trap $hour^{-1}$ in each wood, when an ANOVA was carried out (n=49, F-ratio=1.28, p>0.1).

Total sweep net numbers from each woodland are shown in Table 5.2. Sample numbers were corrected for the number of transects and microhabitats sampled per wood, and an ANOVA of average number of insects per $1000m^3$ of sampled air shows that there was no significant difference between woods (n=51, F-ratio=1.25, p>0.1) (Fig 5.3).

5.3.2.1 The suction trap

The families which occurred most commonly in the suction trap included several nematocerans (Diptera). The sub-order Nematocera (or thread horns)

contains primitive flies. They generally have small, slender bodies and many have the habit of swarming, particularly during the evening (Chinery, 1977). Nematocerans captured in the suction trap included:

- Cecidomyiidae

  Cecidomyiids are small delicate insects. Many of the larvae of these species induce gall formation in plants although the larvae of a few are predatory on other insects (Colyer and Hammond, 1968).

- Ceratopogonidae

  These are tiny flies (Colyer and Hammond, 1968); they rarely exceed 5mm in length (Chinery, 1977). The larvae are mainly aquatic, however, some can be found in alternative habitats such as under the bark of trees (Colyer and Hammond, 1968).

- Chironomidae

  The chironomids (non-biting midges) vary in winglength from 0.7mm to 8mm (Coe *et al.*, 1950). The habit of swarming is very highly developed in these flies and this is done by males, particularly in sheltered areas near water. Immature stages are mainly aquatic although some develop in moss, rotten wood or decaying matter. Some chironomids are described as photophilic e.g. *Orthocladius sordidellus* (Coe *et al.*, 1950).

- Psychodidae

  The Psychodidae are commonly known as owl midges. They are minute flies (Colyer and Hammond, 1968) the adults of which are found throughout spring and summer in large numbers near their breeding places. Larvae are mainly found in aquatic habitats, but, cow dung, sewage works and wet decaying matter are also used (Coe *et al.*, 1950).

Other insects trapped in the suction trap included:

- Lepidoptera, many of which were from the microlepidopteran group.

  Microlepidoptera is the name given to a large group of generally small moths. The 'micros' include the superfamilies Micropterigoidea, Eriocranioidea, Incurvaroidea and Nepticuloidea. The grouping is not based on phylogenetic links, rather a difficulty with identifying many small and often indistinctive species (Chinery, 1977).

- Neuroptera
  - Chrysopidae

    Neuroptera (lacewings) are generally crepuscular and most species are arboreal (Fraser, 1959). They are equipped with hearing organs and have been recorded taking evasive action against attempted capture by foraging bats (Miller and Surlykke, 1995).

- Hemiptera
  - Aphidoidea

    Aphidoidea are minute (2-3mm body length) homopteran bugs and are often brown or green in colour (Chinery, 1977).

- Hymenoptera
  - Chalcidoidea

    Chalcidoidea is a superfamily of small hymenopterans almost all of which are parasites or hyperparasites (Chinery, 1977).

See Table 5.3 for proportions of total suction trap catch attributable to different taxa (dominant families only, see Appendix I for more details).

Table 5.3 **Taxa caught in the suction trap, March to September 1995** (n=4787)

Class	Order	Superfamily	Family	% of Total
Arachnida	Araneae			0.2
Insecta	Coleoptera			1.0
	Diptera		Cecidomyiidae	48.3
			Ceratopogonidae	1.8
			Chironomidae	7.1
			Mycetophilidae	0.6
			Psychodidae	25.1
	Hemiptera		Cicadellidae	0.6
		Aphidoidea		2.3
	Hymenoptera	Chalcidoidea		0.7
			Braconidae	0.6
	Lepidoptera		Geometridae	0.4
		Tineoidea		1.1
		Micromoths		1.2
	Neuroptera	Chrysopidae		1.7
	Psocoptera			0.8

5.3.2.2 Light trap

Table 5.4 shows a breakdown of the major taxa caught in the light trap. Some taxa were similar to those found in the suction trap. Nematoceran Diptera trapped included Cecidomyiidae, Chironomidae and Psychodidae. Nematocera found in relatively large numbers in the light trap but not in the suction trap included:

- Mycetophilidae

  These are delicate flies which often show a preference for dark or damp places where there is decaying matter or fungi. Their popular name,

fungus gnats, describes this predilection. Dancing swarms of males form in some species (Colyer and Hammond, 1968).

Table 5.4 **Taxa caught in the light trap, March to September 1995** (n=6261)

Class	Order	Superfamily	Family	% of Total
Arachnida	Araneae			0.5
	Opiliones			1.7
Insecta	Coleoptera			3.8
	Dermaptera			0.3
	Diptera		Cecidomyiidae	2.2
			Chironomidae	13.5
			Mycetophilidae	1.6
			Psychodidae	1.0
			Tipulidae	3.1
			Empididae	1.8
	Hemiptera		Cicadellidae	1.6
		Aphidoidea		8.9
	Hymenoptera		Braconidae	1.2
			Formicidae	4.3
			Ichneumonidae	1.9
		Chalcidoidea		1.1
	Lepidoptera		Arctiidae	1.1
			Geometridae	3.7
			Noctuidae	13.8
		Micromoths		>13.6
	Neuroptera			0.5
	Trichoptera		Limnephilidae	0.9

- Tipulidae

  Tipulids are slender bodied narrow winged flies with delicate legs which break off easily. Many larvae are terrestrial, although some in the *Tipula*

genus are semi-aquatic, and a few are associated with tree bark or decaying wood (Colyer and Hammond 1968). Tipulids are weak fliers (Service, 1973a).

The only non-nematoceran dipteran family found in large numbers in light trap samples was:

- Empididae

  Empididae larvae develop in decaying vegetation. The adult males of some species form dancing swarms and for this reason the Empididae are sometimes called "Dance Flies" (Chinery, 1977).

Non-dipteran invertebrates captured in the light trap included:

- Opiliones

  Harvestmen are terrestrial nocturnal arachnids (Sankey and Savory, 1974). Sankey and Savory (1974) describe harvestmen as negatively phototactic. Most of individuals were captured in the Long Itchington light trap and belonged to the species *Leiobunum rotundum*. This species is very common and often descends from tree trunks and walls at night to hunt for food in the field layer (Sankey and Savory, 1974).

- Coleoptera
  - Scarabaeidae

    Scarabid beetles include the chafers and dung beetles.

- Hymenoptera
  - Formicidae

    There are 36 species of these social ants present in Britain. Emergence of winged forms usually occurs on one or two days per year when mating takes place in sexual forms (Chinery, 1977).

- Ichneumonidae

  Ichneumonidae are mainly parasites of lepidopteran larvae. Eggs are laid internally within the host or outside the host with larvae feeding from the outside (Chinery, 1977).

- Hemiptera
  - Aphidoidea
  - Cicadellidae

    Cicadellidae are leaf hoppers. They are small insects and can jump and fly readily (Chinery, 1977).

- Trichoptera
  - Limnephilidae

    Limnephilidae are brown caddis flies the larvae of which live, usually, in slow moving water (Chinery 1977)

- Lepidoptera
  - Noctuidae
  - Geometridae

    Geometrids and noctuids are equipped with hearing organs. In the noctuids these are present on the metathorax, and in the geometrids they are situated on the abdomen (Chinery, 1977). Taylor, French and Woiwood (1978) in a study of urbanisation in Britain found large numbers of moths in light traps with the Noctuidae and Geometridae forming the largest groups.

5.3.2.3 Sweep net

Sweep net samples were taken by sweeping across the top of understorey vegetation, then 1m above and finally in an arc above the sweeper. The resulting samples have high numbers of invertebrates which are normally not found in the

aerial fauna but may be available to some species of bat because they are present on vegetation surfaces. Hollyfield (1993), for example, found a relatively high percentage of Araneae occurring in the faecal samples of *M. mystacinus*. 11.75% of individuals caught in the sweep net belonged to the Araneae. Table 5.5 outlines the major taxa caught in the sweep net. These included:

- Araneae
- Collembola (springtails)

  These minute insects are unable to fly. They generally live in soil, leaf litter and vegetation and rarely exceed 5mm in length (Chinery, 1977). McAney *et al.* (1991) do not mention the insect order Collembola as having been identified in bat droppings and it is unlikely that they would normally be available as prey for foraging bats
- Coleoptera
  - Chrysomelidae

    These small leaf feeders are commonly called leaf beetles (Chinery, 1977).
  - Coccinellidae

    This family contains the ladybirds. Most are predatory and many are brightly coloured to warn potential predators of their bitter taste (Chinery, 1977).
  - Nitidulidae

    These small scavenging beetles are often found under bark or in decaying matter (Chinery, 1977).
- Dermaptera

  Only two species of earwig are common in Britain. They are generally nocturnal (Chinery, 1977).
- Diptera: Cecidomyiidae, Chironomidae, Psychodidae, and
  - Agromyzidae

There are about 90 British species of Agromyzidae, the larvae of which are all leaf miners (Chinery, 1977).

- Chloropidae

  The Chloropidae are small or minute insects and most of the larvae are herbivorous (Chinery, 1977).

Table 5.5 **Taxa caught in the sweep net, March to September 1995** (n=3388)

Class	Order	Superfamily	Family	% of Total
Arachnida	Araneae			11.6
Insecta	Collembola			6.8
	Coleoptera		Chrysomelidae	2.7
			Coccinellidae	2.1
			Nitidulidae	3.5
	Dermaptera			0.6
	Diptera		Cecidomyiidae	3.6
			Chironomidae	1.8
			Psychodidae	1.2
			Agromyzidae	4.3
			Chloropidae	2.5
	Hemiptera	Aphidoidea		13.6
			Cicadellidae	2.1
			Delphacidae	2.0
			Miridae	2.7
			Nabiidae	3.2
	Hymenoptera	Chalcidoidea		3.9
	Lepidoptera			2.3
	Neuroptera			0.7
	Psocoptera			2.0
	Thysanoptera			2.1

- Hemiptera included: Aphidoidea, Cicadellidae and
  - ♦ Miridae

    The Miridae is a widely dispersed family with representatives found in many different habitats. The majority are plant-feeders (Chinery, 1977).
  - ♦ Delphacidae

    The Delphacidae is a large family with about 70 British species (Chinery, 1977).
- Hymenoptera
- Lepidoptera

Calculated sweep net sample numbers per $1000m^3$ provide an interesting measure of the combined availability of prey on vegetation substrate and in the air.

5.3.3 Dominant families in the suction and light traps

5.3.3.1 Suction Trap

Highest numbers of Ceratopogonidae (45) and Cecidomyiidae (802) were trapped in Tocil Wood. The close proximity of a waterway and wetlands area (Fig 2.1a) probably affects the relative abundance of insect taxa in Tocil Wood. Many of the insects caught there have aquatic larval stages. Highest numbers of Chironomidae were captured in Long Itchington Wood (194). This woodland is not situated near a waterway but it is possible that the types caught here had terrestrial larval forms.

Psychodidae were most plentiful in Roughknowles Wood (503). Most of these flies were present on the night of 22/6. The woodland is situated beside permanent pastures which may have been the site of a mass emergence of

Psychodidae. Some psychodids are known to have larval stages in dung (Coe *et al.*, 1950).

Aphidoidea were most abundant in Roughknowles (39) and Tocil (45) and in both sites they peaked from mid to late July.

Neuroptera (48) and Lepidoptera (129) were trapped in highest numbers in Long Itchington Wood. The variety of open habitats, with well developed coppicing, and mature wood probably results in a diverse and substantial lepidopteran population. The diversity of vegetation also adds to the range of available habitat.

Hymenopterans were trapped in Tocil Wood (112) in high numbers. These were mainly Ichneumonoidea, the majority of which emerged in mid-July. Ichneumonoidea are mainly parasitic on lepidopteran larvae (Chinery, 1977). Large numbers of Lepidoptera were caught in Long Itchington Wood from mid- to late July, while few Ichneumonoidea were present. In Tocil Wood, however, when the peak in Ichneumonoidea occurred in mid-July, no Lepidoptera were caught in the suction trap. Lepidoptera peaked later in the same month. It is possible that the presence of Ichneumonoidea could, temporarily at least, affect the abundance of lepidopterans present.

5.3.3.2 Light trap

High numbers of Opiliones (harvestmen) were caught in Long Itchington Wood from late July to late August (105).

Coleopterans were captured in greatest abundance in Roughknowles Wood (118) and second highest numbers were caught in Chase Wood (63). Carabids (ground beetles (Chinery, 1977)) were the dominant family in Roughknowles (38). Scarabids were the dominant family in Chase Wood (35). Interestingly, on both 21/5 and 19/7 in Roughknowles Wood, an emergence was

noted of small Scarabaeidae from the field layer in the wood. However, on 21/5 no scarabids were caught in traps, on 19/7 four individuals were captured. This illustrates the difficulty in obtaining a clear representation of available insect fauna, despite the use of several trapping methods.

The dominant dipteran family caught in light traps in each wood were Chironomidae. Empididae were the next highest in both Tocil (39) and Roughknowles (63) but tipulids were more abundant in Long Itchington (106) and Cecidomyiidae were second highest in number in Chase Wood (64).

Hemipterans were found in by far the greatest numbers in Roughknowles Wood, mainly due to a large influx of Aphidoidea peaking in late July with 397 individuals. 463 Aphids were trapped in Roughknowles Wood, in total, whilst the next highest was in Tocil Wood at 79 individuals. Cicadellidae were the dominant hemipteran family present in light trap samples in both Chase Wood (49) and in Long Itchington Wood (21).

Roughknowles Wood exceeded other woods in numbers of hymenopterans trapped (>x5 other woods approximately). The majority of these hymenopterans were winged ants (Formicidae) caught at the end of July (235).

Lepidopterans were trapped in large numbers in Roughknowles (926) and Long Itchington Wood (900).The lowest numbers of lepidopterans were trapped in Tocil Wood (169).

5.3.4 Correlations between insect taxa availability and bat activity

Psychodidae have been found to dominate the diet of 45kHz pipistrelles (Barlow, 1997). This poses the question whether greater activity will be found in woodlands when a high proportion of the fauna sampled consist of Psychodidae, or perhaps other available insect taxa.

However, a problem with conducting statistical tests on taxa data is that many invertebrates were present in large numbers on one night only or were present at most on 5 or 6 nights out of 12 or 13. Only insects families present on 7 nights or more were included in this analysis.

Spearman rank correlations were carried out between average *P. pipistrellus* activity along 100m of the transect in each wood and insect family numbers for each night (per hour or per sweep). Also, peaks in insect availability and bat activity were examined and any patterns noted.

5.3.4.1 Tocil Wood

In Tocil Wood, numbers of: Cecidomyiidae, Chironomidae, and Psychodidae caught in the suction trap (per hour); Chironomidae, Aphidoidea, and Noctuidae from the light trap (per hour) and; Aphidoidea, Chrysopidae, Cecidomyiidae and Chironomidae from the sweep net (per sweep) were used in correlation analysis.

Overall pipistrelle activity along the transect of Tocil Wood was correlated significantly with Cecidomyiidae numbers caught in the suction trap ($n=12$, $r_S=0.60$, $p<0.1$). Activity of pipistrelles in the glade area where both the suction and light traps were situated was correlated significantly with Aphidoidea numbers in the light trap ($n=12$, $r_S=0.57$, $p<0.1$).

Myotis spp activity throughout Tocil Wood was significantly correlated with the number of aphids from the sweep net ($n=12$, $r_S=0.7$, $p<0.05$) and the number of psychodids and cecidomyiids in the suction trap ($n=12$, $r_S=0.57$, 0.67 respectively, $p<0.1$).

5.3.4.2 Roughknowles Wood

Insect taxa used in analysis were: number of Cecidomyiidae, Chironomidae and Psychodidae caught in the suction trap (per hour), and number of Chironomidae, Empididae, Aphidoidea, Geometridae and Noctuidae from the light trap (per hour). Sweep netted insect taxa were not present in sufficient numbers for inclusion.

No significant correlations were found between insect taxa numbers and activity of pipistrelles or *Myotis* spp. in Roughknowles.

The peak in abundance of insects captured in the suction trap occurred on 22/6 (394 individuals). The number of pipistrelle passes also peaked during this night at 115 passes over 5 transects. The majority of insects caught in the suction trap on that date belonged to the family Psychodidae (69%), a prominent constituent of the 45kHz pipistrelle's diet (Barlow, 1997).

5.3.4.3 Chase Wood

Insect taxa used in analysis were: the number of Cecidomyiidae, Psychodidae and Chironomidae caught in the suction trap (per hour); the number of Agromyzidae, Miridae, Cicadellidae and Cecidomyiidae caught in the sweep net (per sweep); and Cecidomyiidae, Chironomidae, Tipulidae, Cicadellidae, Ichneumonoidea, Geometridae and Noctuidae caught in the light trap (per hour) were analysed.

Overall pipistrelle activity was significantly, positively correlated with the numbers of Cecidomyiidae and Psychodidae captured in the suction trap (per hour) and to the number of Geometridae moths present in the light trap (per hour). The r_S values: 0.77, 0.62 and 0.79 ($n=12$, $p<0.05$, $p<0.1$, $p<0.05$, respectively).

Pipistrelle activity in the glade area where the light and suction traps were situated overnight, was significantly correlated with Cecidomyiidae and Psychodidae numbers in the suction trap, Geometridae in the light trap and the number of Agromyzidae from the sweep net (r_S values: 0.78, 0.73, 0.80, 0.69, respectively, n=12, $p<0.05$).

Myotis spp. activity in Chase Wood was correlated with the number of Agromyzidae caught in the sweep net and the number of Cecidomyiidae caught in the sweep net (r_S=0.78, 0.66, n=12, $p<0.05$)

5.3.4.4 Long Itchington Wood

Insect families included in this analysis were: number of Cecidomyiidae, Chironomidae and Psychodidae caught in the suction trap (per hour); Chironomidae, Tipulidae, Geometridae and Noctuidae caught in the light trap per hour; and Cicadellidae and Miridae caught in the sweep net (per sweep).

Activity of *P. pipistrellus* along the whole transect in Long Itchington Wood was significantly correlated with the number of Miridae caught in the sweep net (r_s 0.70, $p<0.1$). Pipistrelle activity in the clear-cut where the suction trap and light trap were situated, was correlated with Cecidomyiidae and Psychodidae numbers in the suction trap and with Geometridae numbers in the light trap (n=10; r_S=0.84, 0.73, 0.72 where $p<0.05$, $p<0.1$, $p<0.1$ respectively). This is very similar to the results from the Chase Wood glade.

The overall peak of pipistrelle activity in Long Itchington Wood was not well defined compared to the three other woods, but the maximum number of observed bat passes occurred on the night of 20/7. On this night the total number of insects caught in the suction trap and the temperature were lower than the preceding night of surveying (despite the positive correlation between maximum temperature and pipistrelle activity, Table 6.4). The proportion of Lepidoptera

caught in the suction trap on that date was higher than the previous night at 18.44%. Pipistrelles may have been availing themselves of high Lepidoptera numbers, resulting in high activity, despite the low temperature.

5.3.5 Diversity of trap samples and bat activity

There are several important points to consider when carrying out analysis with Simpson's diversity index. The index was initially described by Simpson as a measure of concentration. It is an estimate of the likelihood that two individuals picked randomly from a population will be of the same species (in this case family). When 1 is divided by the index, the higher the resulting number, the greater the diversity of a population (Pielou, 1975).

A problem arose when, early in the season, few animals were trapped and these belonged to different families. Then as numbers increased during the season the index sometimes dropped indicating an increase in dominance of one or two types (e.g. Cecidomyiidae or Psychodidae), despite an increase in the number of different families. This results in negative correlations with bat activity because bat activity was greatest during the warm and insect abundant occasions which may have recorded as having a comparatively low index.

Spearman rank correlation analysis was carried out between Simpson's diversity indices of trap samples and pipistrelle or *Myotis* spp. activity for each night in each woodland.

Myotis spp. activity was correlated with diversity in the suction trap in Roughknowles Wood ($n=12$, $r_s=-0.73$, $p<0.1$). Pipistrelle activity was not correlated with diversity from any trap in any of the four woodlands.

An ANOVA was carried out comparing diversity indices, for each night of field work, between woodlands. Indices from each trapping method were analysed separately. Sweep net sample diversity was the same ($n=51$, F-

ratio 0.1403, $p>0.1$) in each woodland. Suction trap diversity was also the same in each woodland ($n=45$, F-ratio=0.50, $p>0.1$). However, diversity from light trap samples each night were different at a 10% significance level ($n=49$, F-ratio=2.24, $p<0.1$). Roughknowles had the highest mean diversity index (least square), 10.2. Long Itchington had the lowest mean at 5.3 and Chase and Tocil Wood had similar means at 8.5 and 8.6 respectively. The highest mean diversity in Roughknowles Wood was probably due to the high number of individuals trapped at the end of July (see Fig 5.2).

5.3.6 Changes in P. pipistrellus *activity during the night (1995)*

5.3.6.1 Tocil Wood (Fig 5.4)

- *Pipistrelle activity*

  Activity was minimal until 20/5. On nights preceding parturition (estimates of times of parturition and lactation taken from Maier (1992) and Swift (1980)) (20/5, 3/6), activity appeared to be unimodal, although the peak was centred on the middle of the night rather than directly post-dusk. On two nights which may correspond to post-parturition and lactation, 21/6 and 1/7, there were distinctive post-dusk and pre-dawn peaks in bat activity. On the night coinciding approximately with the time of weaning, 18/7, activity was very high throughout the night although there were small post-dusk and pre-dawn peaks. Activity was intermittent throughout the nights following weaning (28/7, 20/8), and in late August (29/8) activity became unimodal again with a post-dusk peak followed by a gradual decline. On the final night of surveying in Tocil Wood (14/9) temperatures had increased to a night time average of 11.9°C (from an average of 8.9°C on 29/8) and activity was, again, intermittent throughout.

- *Insects and bat activity*

  Some graphical correlation was found between pipistrelle activity and insect abundance during the nights of 21/6 and 18/7. On all dates there was an initial decrease in insect numbers following sunset, this was ensued, on some occasions, by a pre-dawn peak. On 21/6 bats and insects were particularly well correlated.

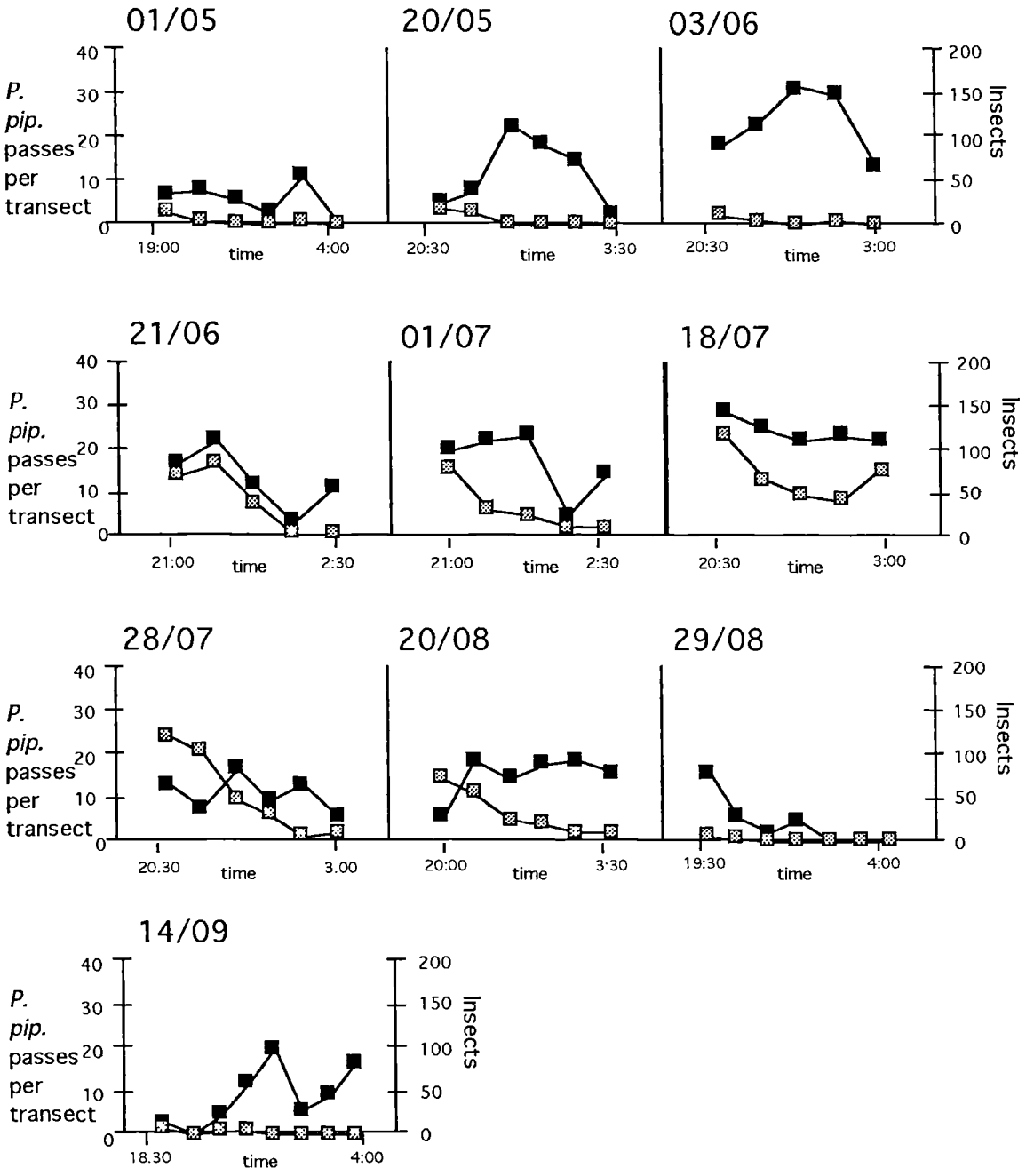


Fig 5.4 Nocturnal *Pipistrellus pipistrellus* activity and insect availability (from the suction trap), Tocil Wood, 1995

- ▩ Number of insects caught in the suction trap during time taken to cover transect
- ■ Number of *P. pipistrellus* passes from each transect

5.3.6.2 Roughknowles Wood (Fig 5.5)

- *Pipistrelle activity*

  Activity in Roughknowles Wood was quite different from Tocil. No maternity roosts were found near this woodland (see Fig 3.2) and this may be the reason why peaks in activity were not observed during the first transect. During pre-parturition/pregnancy survey nights (21/5, 2/6) a peak in activity was recorded early in the night (post-dusk) and again pre-dawn. On 2/6 the pre-dawn peak was higher than the post-dusk. Around the estimated time of parturition (22/6) activity was very high during the night and low at dusk and dawn. At the end of June (29/6), at a time which may have coincided with lactation, a peak in activity was observed at dusk and again at dawn with the dusk peak lower than the dawn peak. However, activity was very low on this night with a total of 16 passes recorded over 5 transects. This low activity may be a function of an inability among lactating bats to move far from the roost to forage (Racey Speakman and Swift, 1987). Lactation/weaning probably took place around mid-July and at this time (19/7), a peak in activity occurred in the middle of the night. On 30/7 activity was fairly evenly distributed with a small peak at dawn although from that night onwards (30/7) activity was quite low. On 18/8 a peak in activity occurred after dusk and activity declined during the night.

- *Insects and pipistrelle activity*

  On 3/5, 22/6, 29/6, 19/7 and 30/7 there did not appear to be any correlations between bat passes and insect numbers. The insect numbers peaked just after dusk and were not utilised by bats. On the first 4 dates mentioned above, insect numbers first increased and then decreased, however on 30/7 there was an initial peak in abundance followed by a second peak

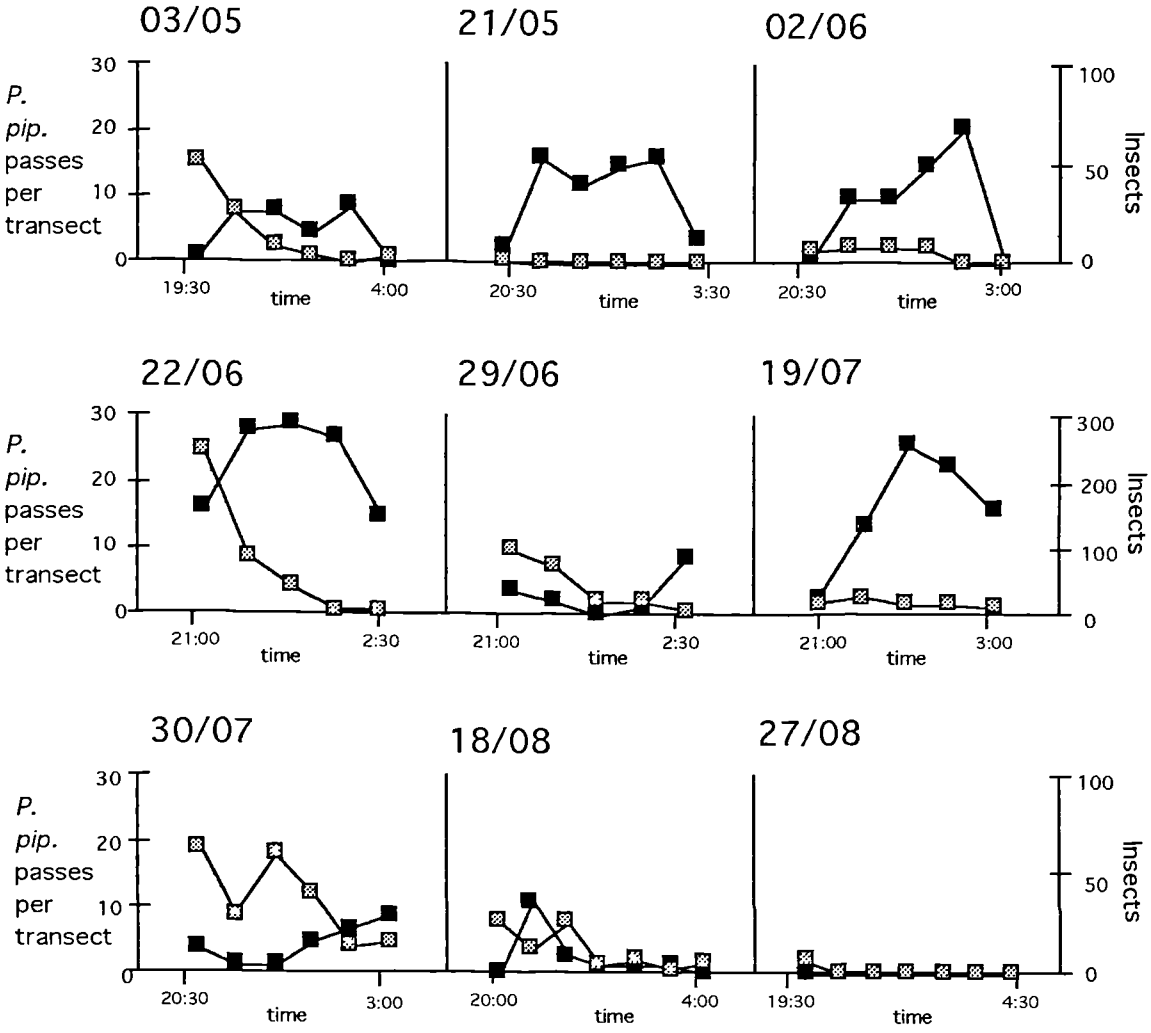


Fig 5.5 Nocturnal *Pipistrellus pipistrellus* activity and insect availability (from the suction trap), Roughknowles Wood, 1995

- Number of insects caught in the suction trap during time taken to cover transect
- Number of *P. pipistrellus* passes from each transect

during the middle of the night. The only night during which there may have been some correlation between bat passes and insect numbers was on 18/8 when bat and insect peaks were similar and tailed-off together.

5.3.6.3 Chase Wood (Fig. 5.6)

- *Pipistrelle activity*

  Observations of pipistrelle passes were scarce on the nights of surveying before 23/5. In early pregnancy, activity was either evenly spread during the night (as on 1/6) or peaked during the night (23/5). Around the time of parturition (19/6) activity also peaked during the middle of the night. During the times roughly corresponding to lactation and weaning (30/6, 17/7) activity followed a bimodal pattern, peaking at dusk and again before dawn. The bimodal pattern became less distinct post weaning, activity was more evenly distributed (27/7, 19/9, 26/8). On the final night of surveying (17/9) only one pipistrelle bat pass was recorded.

- *Insect and bat activity*

  Insect numbers in the suction trap showed a generally declining trend from dusk throughout the night. On 30/6, 17/7, 27/7 and 19/8 *P. pipistrellus* activity and insect numbers were moderately correlated (graphically) during the night.

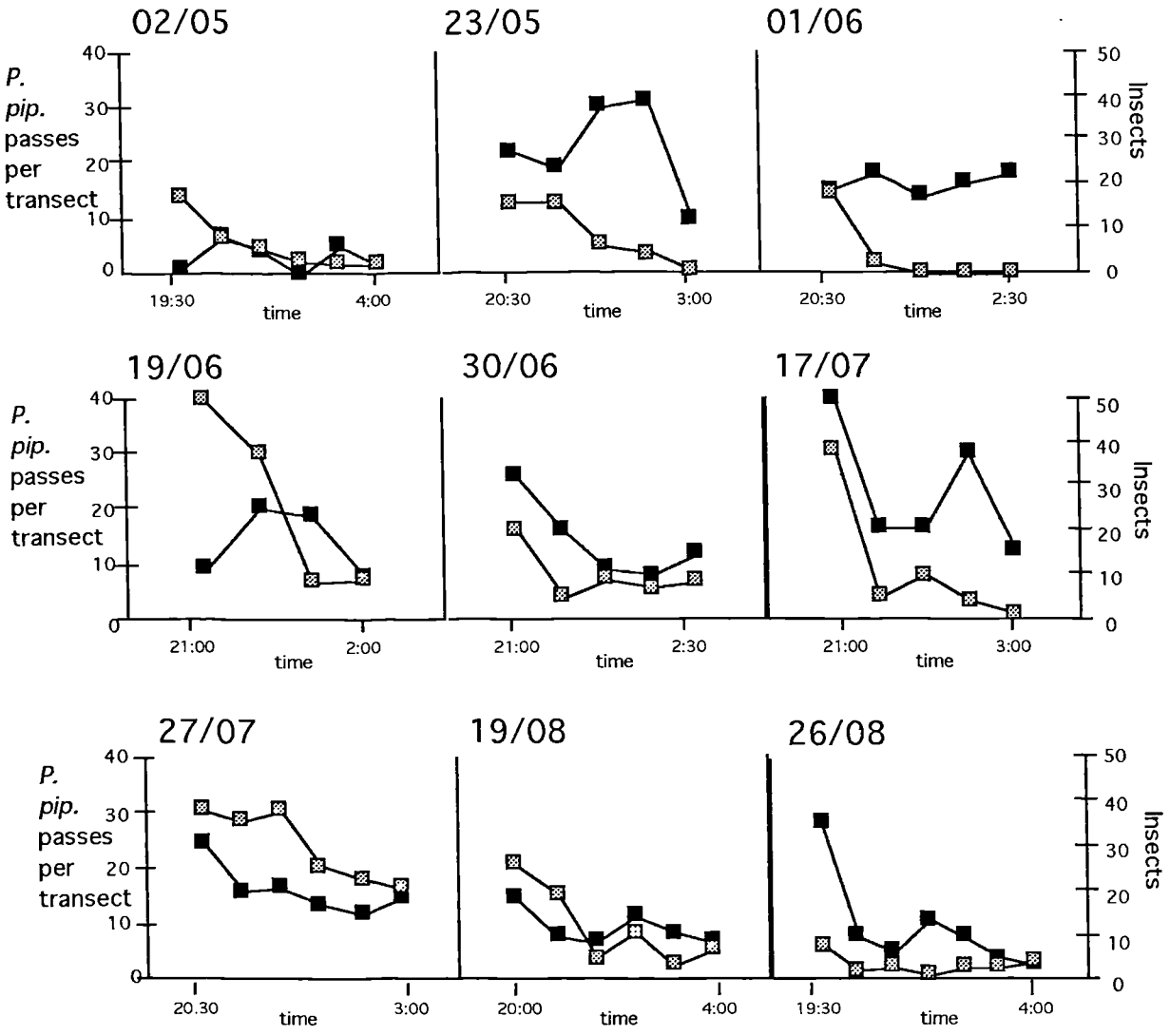


Fig 5.6 Nocturnal *Pipistrellus pipistrellus* activity and insect availability (from the suction trap), Chase Wood, 1995

- Number of insects caught in the suction trap during time taken to cover transect
- Number of *P. pipistrellus* passes from each transect

5.3.6.4 Long Itchington Wood (Fig 5.7)

- *Pipistrelle activity*

Too few transects were covered in Long Itchington Wood during mid-summer to examine nocturnal activity patterns there in detail.

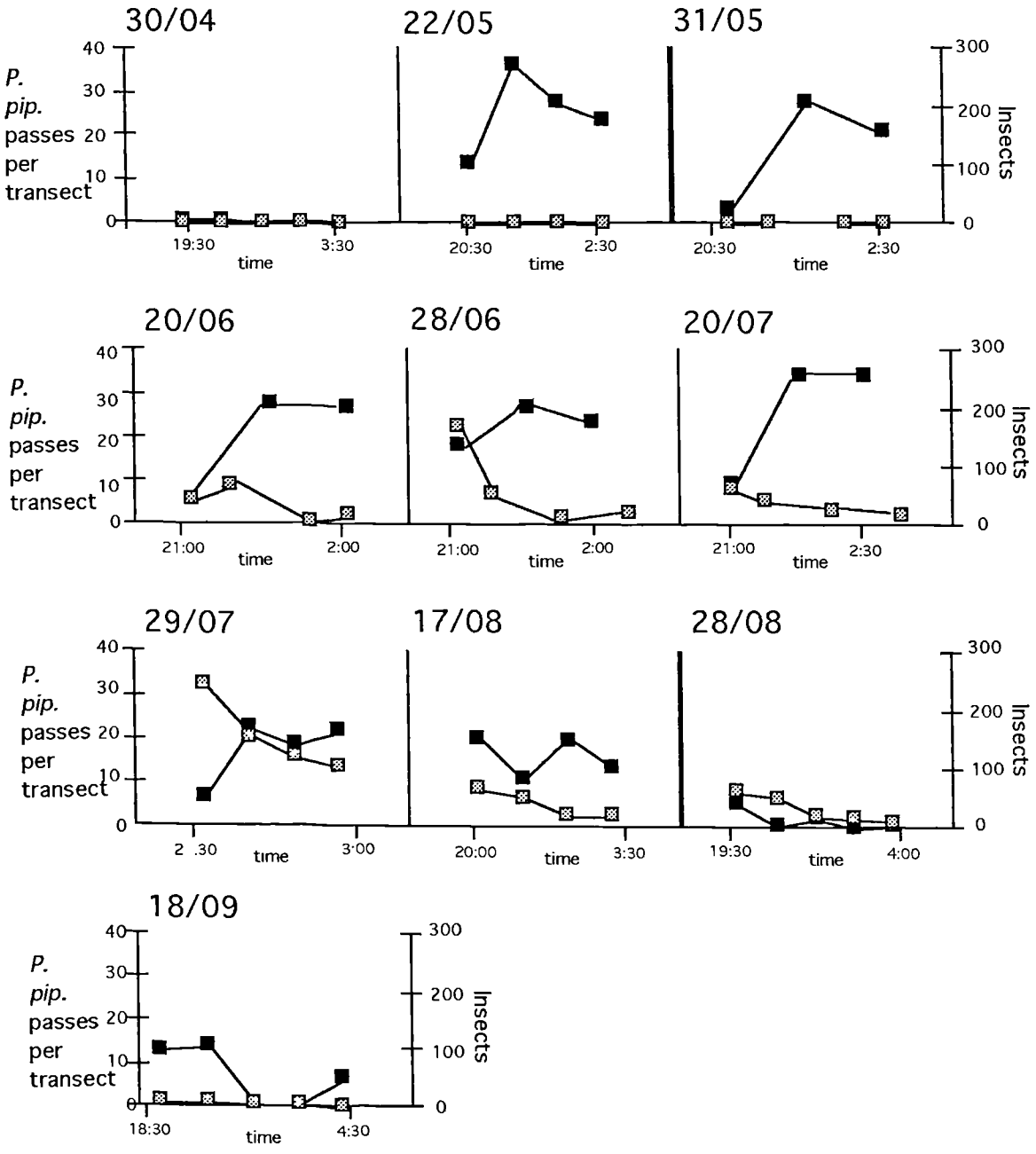


Fig 5.7 Nocturnal *Pipistrellus pipistrellus* activity and insect availability (from the suction trap), Long Itchington Wood, 1995

- Number of insects caught in the suction trap during time taken to cover transect
- Number of *P. pipistrellus* passes from each transect

- *Insect and bat activity*

  The last few study nights in Long Itchington showed a peak in pipistrelle activity during the first transect, followed by a trough and a final peak either during the penultimate or final transect. On 17/8 and 28/8 bat activity and insect availability were graphically correlated, both showed the same declining trend during the night with one or two peaks.

5.4 Discussion

5.4.1 Invertebrate catches

Williams (1939) found that mean abundance in light trap samples peaked in July during his trapping survey. In this study, light trap numbers peaked during August and suction trap numbers in July in three of the study woodlands. In Roughknowles, peaks occurred during preceding months. The earlier peaks in Roughknowles, compared with the other three woodlands, may have been because of its open canopy. The field layer was easily warmed by heat from the sun and this would have facilitated earlier insect emergences than in other more densely vegetated woodlands. Vegetation of the shrub and field layer are influenced by the amount of light and shade from the canopy layer, and this affects insect life (Neal, 1958).

Sample numbers were quite variable between woodlands, although this was not supported by results from the ANOVA. Despite a lack of statistical significance it was apparent that a lower number of insects were caught in the suction trap in Chase Wood (see Fig 5.1). Chase Wood is maintained for pheasant hunting. Kirby (1992) noted that the higher the number of pheasants in a wood the greater the chance of damage to the invertebrate fauna. Pheasants were

present throughout 1995 in Chase Wood and were often disturbed from their night time perches, although no attempt was made to estimate the density of the population. Open grassy areas were maintained in Chase Wood at the expense of naturally occurring field flora. The woodland is also situated on a south facing slope, this may result in a convergence of aerial fauna at the bottom of the wood where sampling did not take place. Despite the relatively depauperate suction trap fauna, bat activity was not lower than at the other study sites (see section 4.3.2).

The light trap caught fewest insects in Tocil Wood. There are two possible reasons for this: dense vegetation in the glade area where the light trap was situated reduced its catchment area and, the trap was situated at a distance of approximately 20m from a footpath lit by white lights. This may have contributed to reducing the catchment area, similar to moonlight effects (see section 1.3.4).

The light trap in Roughknowles Wood probably had the greatest catchment area of all four woodlands. This site was more exposed than the other three. Taxonomical diversity of captures in the light trap was greatest in Roughknowles Wood.

Taxa were caught in different proportions in each trap. This phenomenon is well documented (Southwood, 1978). The light trap was most efficient at capturing lepidopterans while the suction trap caught high proportions of Diptera. In the sweep net, catch samples were more evenly distributed among orders, although hemipterans were most common.

There were examples of peaks in insect family abundance occurring on different dates in the light and suction traps. For example, in Long Itchington Wood, the peak in Chironomidae caught in the suction trap was 69 individuals captured on 29/7 and in the light trap the peak occurred on 28/8 with 94

specimens. This may be because individuals belonging to the same species are only attracted to the light trap during a certain stage in their life cycle, or it is possible that different species in the same family were attracted to the light trap: some Chironomidae are known to be photophilic (Coe *et al.*, 1950).

Cecidomyiidae were the most commonly trapped insect family in the suction trap. This is unsurprising given their small size and life cycle. The larvae of many species are very common in woodlands. Their small size and weak flight almost guarantees capture in the suction trap. In a study of the nocturnal aerial insect fauna of Tocil Wood in 1994, using the suction trap, Cecidomyiidae composed 71% of insects captured (Eliot-Higgit, 1994).

Psychodids were captured in large numbers in the suction trap for similar reasons. Chironomidae, however, were not particularly abundant compared with other studies (e.g. Swift *et al.* (1985) found that they composed over 50% of the sampled aerial insect fauna). The larvae of these insects are mainly aquatic and because three of the study sites were not close to waterways, they were not expected to be present in large numbers.

The most common Lepidoptera present in light trap samples were the Noctuidae and Geometridae. Geometrid caterpillars feed mainly on the foliage of trees. Adults geometrids, although more active during the day than Noctuidae, are often attracted to light traps (South, 1961b). The Noctuidae larvae feed at night in foliage and the adults are almost all night flyers. Some are readily attracted to light (South, 1961b).

Hemipterans were the most common insect in sweep net samples. Most of the hemipteran families captured in the sweep net were also caught in the suction trap which means that, although many may have been resting or feeding on vegetation, they occasionally compose part of the aerial insect fauna (e.g. Aphidoidea, Cicadellidae).

5.4.2 *Pipistrelle diet and activity*

Nematoceran flies have been found in large quantities in *P. pipistrellus* faeces (Barlow, 1997; Sullivan *et al.*, 1993; Swift *et al.*, 1985), although, not necessarily in larger proportions than available (Swift *et al.*, 1985). While positive significant correlations were found between cecidomyiid availability and *P. pipistrellus* activity in this study, it is possible that these were indicative of some other relationship. Cecidomyiidae have been found to be eaten in only very minute quantities by 45kHz pipistrelles (Barlow, 1997). 45kHz pipistrelles were the type most commonly encountered in this study (see section 4.3.1). However, cecidomyiidids have soft bodies and this may render identification in droppings difficult. Also, previous studies (Sullivan *et al.* 1993; Swift *et al.*, 1985) have not been carried out specifically around woodlands so Cecidomyiidae may not have not been so abundant.

Psychodidae have been noted as an important prey type of the 45kHz pipistrelle (Barlow, 1997). Spearman's analysis showed some correlation between Psychodidae numbers and pipistrelle activity. In Roughknowles Wood, where no statistically significant correlation was found, the pipistrelle activity peak coincided with a peak in Psychodidae availability. However, here also, associations between psychodids and pipistrelles may reflect some other correlation.

In Chase and Long Itchington (glade and clear-cut), a significant correlation was found between Geometridae numbers (from the light trap) and pipistrelle activity. Although lepidopteran remains are occasionally found in pipistrelle faeces they have not been noted as an important prey group (e.g. Barlow, 1997).

Aphids, also, have not been recorded as an important prey item for pipistrelles, although there is a possibility that aphids that had passed through

the gut of a bat would not be recognisable because they have very soft bodies and delicate wings. Aphidoidea may have had an important effect on pipistrelle activity in Tocil Wood. The numbers caught in the light trap (per hour) correlated with pipistrelle activity in the natural glade. This was illustrated on the last survey night in Tocil Wood when activity was quite high and the only insect taxa available in reasonably large amounts were Aphidoidea (light trap).

The prey eaten by a species may be dependent upon local availability (McAney and Fairley, 1989). Barlow (1997) found that Anisopodidae were an important diet constituent in faeces from two roosts, but not in another.

While there may have been some correlations between availability of certain prey types and pipistrelle activity, it seems that on the whole, prey abundance is a more important factor (see also Chapter 6). Average *P. pipistrellus* activity was similar throughout all four woods (see section 4.3.2) despite the variation between woods in available prey taxa. This supports the hypothesis that *P. pipistrellus* has an opportunistic foraging style and that bats will avail themselves of local prey specialities.

5.4.3 Nocturnal activity

Nocturnal pipistrelle activity data from this study showed similar trends to those found in roost emergence studies (Swift, 1980; Maier, 1992) in two out of the three woodlands examined in relation to activity patterns.

The trends of activity found in Tocil Wood and Chase Wood may reflect their proximity to maternity colonies (see Fig 3.2). In this investigation, activity during the night was often more extended than in Scotland (Swift, 1980) and this is likely to have resulted from the extremely hot weather during the summer of 1995. Maier (1992) found that activity was prolonged throughout the night when

temperatures were high. Summer nights are also longer in central England compared with Scotland, allowing protracted activity.

Roost counts provide a direct measure of how many bats are active. However, the activity of echolocating bats may not be directly proportional to the number of bats in a nearby roost. It is possible that bats may use an area for foraging at some period during the night and then move away to another site rather than return to the roost. It is also likely that some of the individuals observed are males or females unassociated with maternity roosts (compared to the two studies mentioned above).

While bats may move from site to site while feeding, it is unlikely that they would all move en masse to the same sites. Dispersal from the roost is an important strategy to allow maximum intake of food with a minimum commuting distance. The foraging flights of *Tadarida brasiliensis* (Mexican free-tailed bat) are dispersed throughout a 50-mile radius from their cave roosts (Constantine, 1970). Therefore, when activity trends show a general decline, e.g. from dusk to dawn, this probably represents a gradual return of flying bats to their roosts.

Maier (1992) found that, pre-parturition, activity was often attenuated during the night and this was also the case in both Chase and Tocil Wood. During periods corresponding to post-parturition and lactation, activity was bimodal with distinctive post-dusk and pre-dawn peaks. In both woodlands, the pattern became unimodal by late August. These trends were comparable to those found by Maier (1992).

No roosts were found in close proximity to Roughknowles Wood. Activity here was not similar to that found by Swift (1980) or Maier (1992). For example, there were few bat passes observed on a night corresponding to lactation. Racey *et al.* (1987) found that the average direct distance of sightings of marked bats

from the roost was 1.8km before parturition and 1.3km after parturition. The reduction in travelling distance during lactation may reflect increased commuting costs associated with returning to the roost in the middle of the night (Racey *et al.*, 1987)

Insect abundance during the night was not always correlated (graphically) with relative pipistrelle activity. Although some correlations were found (see Table 6.4) between overall abundance of insects in the suction trap and activity in woodlands, it did not follow for hourly changes in activity.

Correlations between activity during the night and abundance in the suction trap were not noted until late June in three of the woodlands (Roughknowles, Tocil and Chase). This may have been the result of lactating mothers returning to roost during the night to suckle young, thereby creating a trough in activity correlated with the dip in insect abundance. It may also reflect the high energy requirements of lactation because it would not benefit lactating mothers to fly where there are few prey available.

In Roughknowles Wood the post-dusk peak in aerial insect availability was rarely utilised. This may have been because of a lack of nearby roosts, or alternatively, bats foraged in Roughknowles later than in other woodlands because the open nature of the woodland exacerbates the threat of predation. Jones and Rydell (1994) noted that emergence times are a function of predator avoidance and the ability of a bat species to utilise the dusk peak in aerial insects, for example, emergence of *P. pipistrellus* from the Keeper's Cottage roost, was earlier than the average for pipistrelles calculated by Jones and Rydell (1994). This was probably due to the close proximity of Chase Wood and its shelter providing canopy (see section 3.4.2.3).

Summary

The work presented above supports the hypothesis that *P. pipistrellus* has an opportunistic foraging style. Where a roost had been located close to a study woodland, *P. pipistrellus* nocturnal activity patterns were similar to those described in other studies.

Chapter 6

THE INFLUENCE OF WEATHER AND INSECT ABUNDANCE ON SEASONAL BAT ACTIVITY IN DECIDUOUS WOODLAND

6.1 Introduction

Bat foraging habits are influenced by many behavioural factors such as the selection of habitat and prey, and duration of feeding bouts, each of which may be changed to optimise efficiency under changing environmental conditions (Anthony *et al.*, 1981).

Climate is an important factor regulating the life strategies of bats. Seasonal fluctuations can bring about such dramatic changes as the onset of hibernation. Microchiropteran bats have evolved tactics to optimise foraging success. Embryonic development between mating during autumn and birth during mid-summer (when arthropod availability is at a peak) is delayed, thus allowing females to meet the high energy demands of pregnancy and lactation (Racey, 1982). Daily weather changes affect small scale activity patterns such as dawn foraging bouts (Rachwald, 1992).

Potential changes in habitat use by either bat or insect species with varying climate is a topic which has been overlooked in the past. Kindvall (1995) deduced that preservation of rare species may only be possible if habitats with a wide range of local climates are maintained.

6.1.1 Weather variables affecting bat and insect abundance

6.1.1.1 Temperature

Bat activity has been recorded in Europe during the winter at temperatures of 7° or 8°C and higher (Corbet & Harris, 1991). Flight activity of bats generally increases with temperature, with flights of shorter duration on cooler nights (Anthony *et al.*, 1981) and extended duration on warmer nights (O'Farrell *et al.*, 1967).

Rachwald (1992) noted an increase in morning foraging by *N. noctula* during warm nights. Distinct peaks of activity disappeared in warm weather.

During nights of low temperatures bats intensified foraging shortly after sunset. The pre-dawn foraging peak that has been noted in many species may be weather related; *Myotis californicus* only forages at dawn on warm nights (O'Farrell and Bradley, 1970).

Walsh and Mayle (1991) observed that there was a positive correlation between bat activity and minimum temperature in areas of woodland with high activity, and no significant correlation between activity and temperature in microhabitats of low activity. It is hypothesised, in this thesis, that temperature may be correlated with bat activity in microhabitats of high activity.

Peng (1991) found that many families of aerial dipterans preferred warm conditions for flight. A preference among insects for warm conditions has been reported by many authors (e.g. Williams, 1940; Wellington, 1945).

Rautenbach *et al.* (1988) suggested that temperature is an important regulator of bat activity, through its effects on insect availability. It is hypothesised in the present study that temperature influences bat activity, mainly through its effects on insect abundance.

6.1.1.2 Humidity

Studies have demonstrated the importance of water balance to bats in the laboratory (Bassett, 1980; Bassett and Weibers 1980), in the roost (Webb *et al.*, 1994; Webb *et al.*, 1995), and in free-flight conditions (Kurta *et al.*, 1989; Kurta, Kunz and Nagy, 1990). Adam *et al.* (1994) found a direct relationship between flight activity of *C. townsendii virginianus* and ambient relative humidity; bats exhibited reduced activity on nights of lower relative humidity. Adam *et al.* suggested that this was a behavioural strategy to prevent excess water loss. This hypothesis is examined in this thesis.

However, Adam *et al.* did not measure insect abundance during their study and it is possible that bats were not directly affected by low humidity,

through physiological requirements, but indirectly, through its effects on insect availability.

Peng (1991) found that many dipteran families flew more readily in dry weather. However, Wellington (1945) found that changes in relative humidity seemed to have little effect upon the average insect under normal flight conditions.

Kindvall (1995) noted changes in habitat requirements of the bush cricket (*Metrioptera bicolor*) in Sweden during an extreme drought. The usual low grassland sites were less frequented and large numbers were observed in unusual habitats such as pine forests.

6.1.1.3 Wind

Strong winds have been found to suppress flight activity in bats by making flight difficult (O'Farrell *et al.*, 1967). An inverse relationship was found between bat activity and windspeed in the study by Adam *et al.* (1994) on *C. townsendii virginianus*.

Windspeed and direction also affects availability of insect prey because insects on the wing often accumulate on the lee side of wind breaks such as tree lines and fences (Lewis 1967; Lewis 1970; Peng 1991; Peng *et al.*, 1992).

The hypothesis that within a sheltered woodland, windspeed may have little influence on either bats or insects is investigated. However, at edges exposed to wind, flight activity may be suppressed and at edges to the lee of windward bat activity may be greater.

6.1.1.4 Barometric Pressure

Paige (1995) noted a negative correlation between *Pipistrellus subflavus* activity and barometric pressure. Paige maintained that the only physical external factor that changes for a bat roosting within a cave is barometric pressure, and pressure is an environmental clue bats could use to predict the abundance of aerial insects outside the roost without expending flight energy

to assess insect activity directly. However, in other studies barometric pressure has not been noted as an important variable regulating bat activity (e.g. Adam *et al.*, 1994; Rautenbach *et al.*, 1988).

Paige (1995) found insect activity to be significantly negatively correlated with barometric pressure. Wellington (1945), however, disregarded barometric pressure as a limiting factor in the aerial distribution of insects.

6.1.1.5 Rainfall

The effects of rainfall on bat activity have varied between studies. Entwistle *et al.* (1996), for example, found flight activity in brown long-eared bats to be reduced during heavy rain while Catto *et al.* (1995) found no activity decrease among *E. serotinus*. Rainfall may interfere with echolocatory capabilities, or among gleaning bats prevent them from listening for prey (Entwistle *et al.*, 1996). The hypothesis that rainfall causes a decrease in bat activity is examined in this chapter.

6.2 Materials and Methods

6.2.1 Field work

For descriptions of study sites, field work dates, bat and insect abundance estimation, see Chapter 2.

6.2.1.2 Weather data

A Phillip Harris portable DL Plus datalogger was used in an open area of woodland on each survey night in 1995. This instrument is mainly used as an educational tool and is not waterproof. It was covered in clear plastic and tied to a support approximately 50cm from the ground. Four associated probes were attached to a 2m high stand measuring: ambient air temperature (°C), light intensity (Log Lux), wind speed (rotations per second) and wind direction (degrees).

Measurements were taken from dusk until dawn at approximately 3 minute intervals. The datalogger is powered using 12 AA batteries. The anemometer was discovered later to be inaccurate in measuring windspeed due to over sensitivity which caused output from the probe to saturate at low wind speeds and data from it were not used.

All information was downloaded to an Apple Macintosh computer using Kermit (0.97) communications software.

Average relative humidity (%) was calculated from four measurements taken during the night using a whirling hygrometer and average cloud cover was calculated from four estimations by eye (%).

Data from Bablake Weather Station (SP 328 795) in Coventry was also used. The following variables were taken from Bablake: maximum temperature (°C), minimum temperature (°C), soil temperature (temp. of grass in 1996) (°C), hours of sunshine, relative humidity (%), windspeed (kmph) and direction, total rainfall (mm) and atmospheric pressure (millibars). Measurements were taken until midnight of the date of data collection from the preceding 24hrs. 1996 weather data were taken from Bablake Weather Station.

6.2.2 Analyses of results

6.2.2.1 Regression analysis

Simple (linear) regression analyses were carried out with weather data as independent (X variables) and bat activity or insect data as dependent (Y) variables. Some data were transformed to conform to the assumptions of homoscedasticity[1] and normality for regression analysis (Zar, 1984). Lilliefors tests were carried out on data lists to ensure normal distribution of samples.

[1] Homoscedasticity is a synonym for homogeneity of variances, where the variance of Y at any X does not increase in proportion to X

Relative percentage humidity was arcsine transformed. Temperature data and hours of sunshine were log transformed (log_{10}) where necessary. Pressure data were found to be normally distributed without any transformations.

P. pipistrellus and *Myotis* spp. numbers of passes per hundred metres of transect (or microhabitat) per night (1995) were regressed against weather variables to determine accurate predictors of activity. Those that achieved a significance of $p \leq 0.1$ were included in a forward stepwise regression model to determine which factors would most accurately predict *P. pipistrellus/Myotis* spp. activity. Probability values to remove and enter a variable from or to the model were set to 0.05. This low value helps to prevent problems caused by multicollinearity (Wilkinson *et al.*, 1992).

When one or more *significant predictors were drawn, these were* verified by using interactive stepping. However, no changes were made to models in this way.

Bat data from all four woodlands were analysed together, then separately and then individual microhabitats were examined with respect to bat activity and climate data.

Insect numbers (1995) were regressed against weather data using the same method as above. Numbers from each trap were analysed separately.

6.2.2.2 Correlation analysis

Multiple partial correlation is a statistical method used to deduce whether the correlation between two variables is due to their dependence on a third variable. The partial correlation coefficient eliminates the effects of other variables. If the correlation coefficients between variables X_1, X_2 and X_3 are r_{12}, r_{13} and r_{23} then the partial correlation coefficient between X_1 and X_2, with X_3 held constant, is

$$r_{12\,3} = \frac{r_{12} - r_{13} \cdot r_{23}}{\sqrt{1 - r_{13}^2} \cdot \sqrt{1 - r_{23}^2}}$$

(Freund and Simon, 1992).

While regression analysis satisfactorily determines the most accurate weather predictors of relative bat activity, the inclusion of insect data as independent variables into these analyses may not be appropriate. One of the prerequisites for regression analysis is that one variable be independent of the other and, while this is likely to be true for bats and weather (with weather independent of bat activity), it may not be the case for insect abundance and bat activity. Insect abundance may not be entirely independent of bat activity, particularly in areas of high bat activity. Correlation analysis was used to compare insect and bat data.

Multiple partial correlations were carried out on 1995 bat data with the most statistically significant weather variable(s) from regression analysis for that microhabitat or woodland, and a measure of insect abundance. This was done to determine if weather variables or insect abundance were correlated with bat activity. If no weather variables had been significantly regressed against bat activity, the relationship between insect trap numbers and activity was analysed using Pearson's correlation.

1996 Chase Wood data was analysed by individually correlating overall *P. pipistrellus* activity in the woodland, and in each microhabitat, with weather variables using multiple partial correlation. To correct for lunar effects, nights of the lunar cycle were numbered from 1 to 15 representing phase of the cycle from new to full (Anthony *et al.*, 1981), and numbers equating the stage of lunar cycle on field work nights were held constant during the analysis.

6.3 Results

Comparing the results of regression and correlation analyses can be difficult because several methods were used to measure insect abundance. Correlations between bat activity and weather variable(s) were sometimes significant using multiple regression but not significant using multiple partial correlation while insect numbers were held constant.

Occasionally, a significant correlation was found between bat activity and a weather variable when one set of trap numbers (e.g. number of insects caught in suction trap $1000m^{-3}$) was held constant (multiple partial correlation) but not when another was held constant. In these cases, it is postulated that bat activity was to some extent affected by insect availability (whether measured by sweep net or suction trap, and which may itself be affected by a weather variable) so a singular direct correlation between the weather variable and bat activity cannot be assumed.

Weather data from Bablake Weather Station usually provided the most accurate predictors of bat activity or insect abundance. When the source of the significant variable was measurements taken within the woodland, this is indicated in Tables 6.1 to 6.9.

6.3.1 1995 Results

6.3.1.1 All four woodlands combined

6.3.1.1.1 *Pipistrellus pipistrellus*

Regression analyses were performed on the combined datasets for all woodland sites. Results showed a significant positive relationship between soil temperature and *P. pipistrellus* activity. A positive relationship was also found between suction trap numbers and soil temperature (see section 6.3.1.1.3). Soil temperature probably fluctuates to a lesser extent than

maximum or minimum temperature. Soil temperature may affect insect emergences and therefore insect availability.

Pipistrelle activity was significantly correlated with light trap and sweep net insect numbers, with soil temperature held constant. The correlation between activity and light trap numbers was negative while the correlation between activity and sweep net samples was positive (Table 6.1).

Table 6.1 **Bat activity from all four woodlands (per night) with significantly regressed and correlated variables**

Y variable	Regressed (X) variable(s)	F-value$_{df}$	Multiple partial correlation: Significant correlate	Variable held constant	r (correlation coefficient)
P. pip.	Soil temp. (+ve)	$13.1_{1\ 46}$***	Sweep net numbers	Soil temp.	0.48***
			Light trap *numbers*	*Soil temp.*	-0.32**
Myotis spp.	Rel. humidity (ve) and Bar. pressure (-ve)	$4.5_{2\ 45}$**	Bar. pressure	Suction & humid	-0.33*
			"	Light trap &humid.	-0.38**
			"	Sweep & hum.	-0.34**
			Sweep net numbers	Humid. &press.	0.50***
			Light trap numbers	Humid. & press.	-0.34**

6.3.1.1.2 *Myotis* spp.

Stepwise regression analysis on *Myotis* spp. activity showed that humidity and barometric pressure, combined, were the most important predictors. The relationships were both negative.

Myotis spp. activity from all four woodlands was significantly correlated with barometric pressure when the effects of humidity and the number of insects caught in each trap were both held constant. With humidity and pressure held constant there was a significant relationship between *Myotis* spp. activity and light trap and sweep net sample numbers. However,

the correlation between light trap numbers and activity was negative (Table 6.1).

6.3.1.1.3 Insect numbers (regression)

The number of insects caught in the suction trap in all four woodlands was most accurately predicted by a positive relationship with soil temperature (n=50, F=68.9, p<0.01) (Fig 6.1).

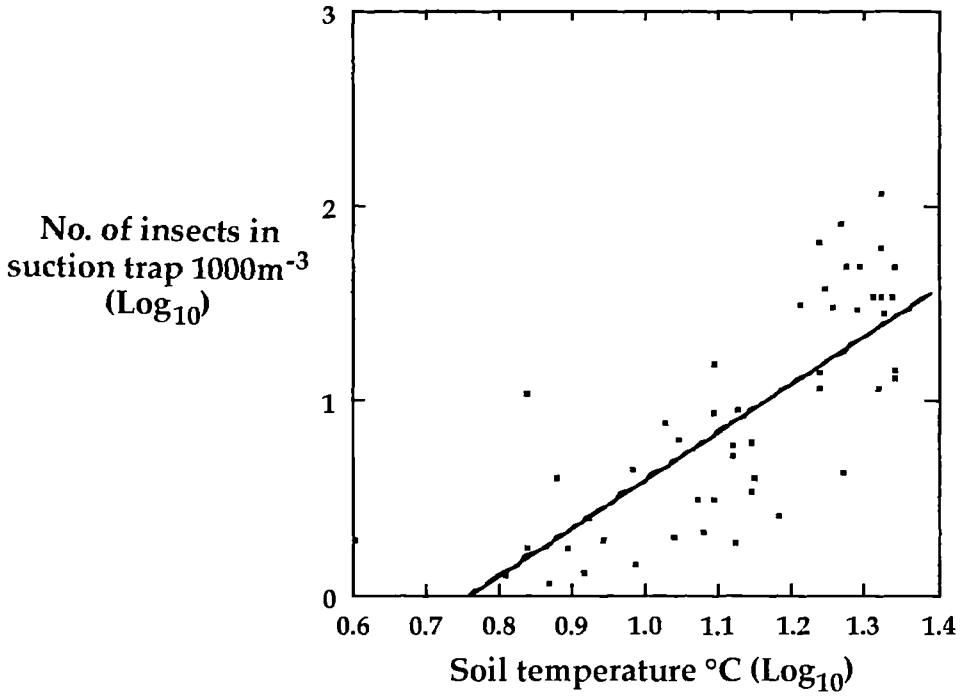


Fig 6.1 Suction trap numbers from all four woodlands 1995 significantly correlated with soil temperature (Bablake), F=68.9, p<0.01.

The number of insects caught in the light trap was also best predicted by temperature, in this case, average temperature measured within the woodland (n=50, F=143.69, p<0.01) (Fig 6.2).

Sweep net numbers were best predicted by a combination of soil temperature and rainfall. The association with temperature was positive (Fig 6.3) and the relationship with rainfall was negative (Fig 6.4) (n=51, F=20.07, p<0.01) (Table 6.2).

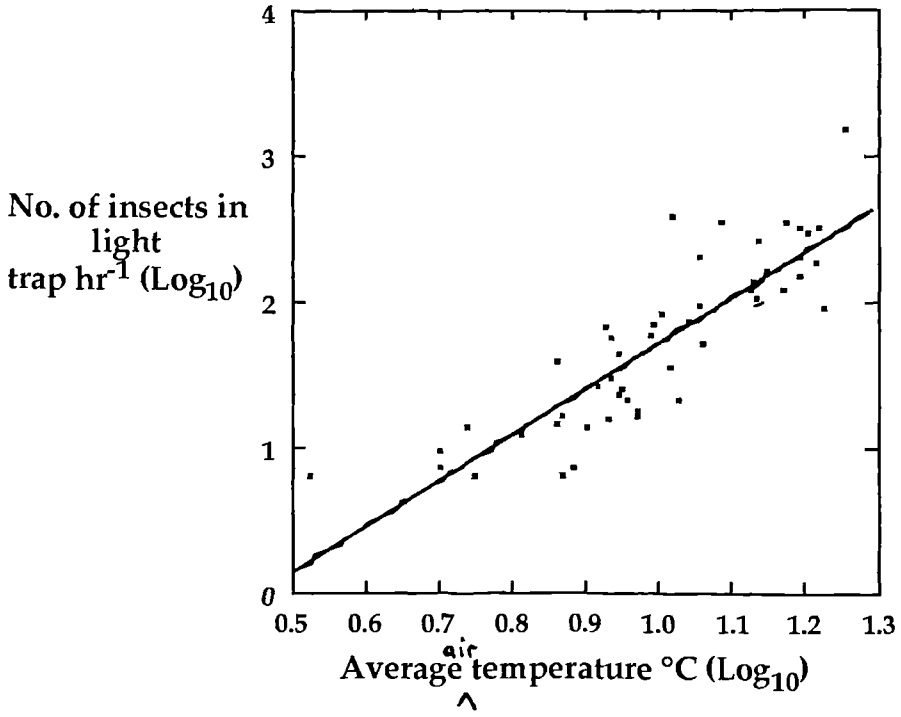


Fig 6.2 No. of insects caught in the light trap in all four woodlands 1995, significantly correlated with average temperature during the night in each woodland, F=143.7, p<0.01

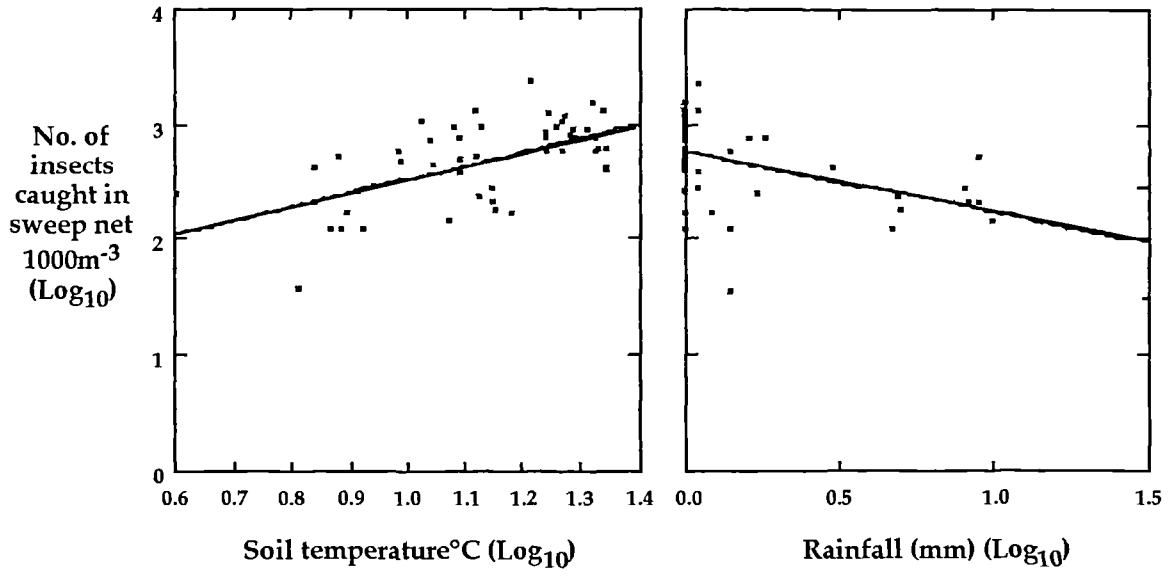


Fig 6.3 & 6.4 Number of insects caught in the sweep net in all four woodlands 1995 signficantly correlated with soil temperature and rainfall, F=20.1, p<0.01

Table 6.2 **Insect abundance from all four woodlands (per night) with significantly regressed climate variables**

Insect trap numbers (Y)	Regressed (X) variable(s)	F-value$_{df}$
Suction trap (1000m^{-3})	Soil temp. (+ve)	$68.9_{1,48}$***
Light trap (per hour)	Average temp. (in wood) (+ve)	$143.7_{1,48}$***
Sweep net (1000m^{-3})	Soil temp. (+ve) and Rainfall (-ve)	$20.1_{2,48}$***

6.3.1.2 Each woodland

Different variables were found to most significantly correlate with relative *P. pipistrellus* and *Myotis* spp. activity in each wood.

Temperature was the most important predictor for insect abundance (numbers per volume sampled suction trap, numbers per hour light trap, and numbers per volume sampled of sweep net). Temperature significantly predicted the number of insects sampled in the suction trap in each woodland except Roughknowles where insect numbers were more accurately predicted by a negative relationship with windspeed (Table 6.3).

Table 6.3 **Insect abundance in each woodland (per night) regressed against climate variables**

Woodland	Insect trap numbers (Y)	Regressed (X) variable(s)	F-value$_{df}$
Tocil	Light	Max. temp. (+ve)	$38.0_{1,11}^{***}$
	Suction	Soil temp. (+ve)	$35.5_{1,11}^{***}$
	Sweep	Soil temp. (+ve) and Rel. Humidity (-ve)	$7.9_{2,10}^{***}$
Roughknowles	Light	Ave. temp. (in wood) (+ve)	$66.0_{1,10}^{***}$
	Suction	Windspeed (-ve)	$26.0_{1,11}^{***}$
	Sweep	Windspeed (-ve) and Bar. pressure (+ve)	$9.3_{2,10}^{***}$
Chase	Light	Soil temp. (+ve)	$88.6_{1,10}^{***}$
	Suction	Soil temp. (+ve)	$13.1_{1,10}^{***}$
	Sweep	Rel. humidity (-ve)	$14.6_{1,10}^{***}$
Long Itchington	Light	Min. temp. (in wood) (+ve)	$56.3_{1,11}^{***}$
	Suction	Soil temp. (+ve)	$55.3_{1,10}^{***}$
	Sweep	Max. temp. (+ve)	$9.5_{1,11}^{**}$

6.3.1.2.1 Tocil Wood

- Regression

  P. pipistrellus activity was predicted by soil temperature (+ve) in Tocil Wood.

  Myotis spp. numbers were not accurately predicted by any weather variable.

- Multiple partial correlation

  A significant correlation was found between soil temperature and pipistrelle activity with the effects of sweep net sample number held constant ($M=3$, $n=13$, $r=0.57$, $p<0.1$). However, temperature may not be an important influence on pipistrelle activity because with suction trap numbers held constant, there was no significant correlation between activity and temperature.

No weather variables were found to accurately predict *Myotis* spp. activity from regression analysis. However, the average number of insects caught in the sweep net significantly correlated with activity (Table 6.4).

Table 6.4 **Bat activity from each woodland (per night) with significantly regressed and correlated variables**

Woodland /species	Regressed (X) variables	F-value$_{df}$	Multiple partial correlation (or Pearson): Significant correlate	Variable held constant	r value$_n$
Tocil *P.pip.*	Soil temp. (+ve)	$10.3_{1,11}$***	No sign. corr. with suction or light trap included	n/a	n/a
Tocil *Myotis*	No predictors	n/a	Sweep net (Pearson correlation)	n/a	0.66_{11}**
Rough *P. pip.*	Bar. pressure (+ve)	$5.1_{1,8}$*	Sweep net	Bar. pressure	0.73_{13}**
Rough *Myotis*	No predictors	n/a	Sweep net (Pearson correlation)	n/a	0.81_{9}***
Chase *P. pip.*	Soil temp.	$5.6_{1,10}$**	Suction trap	Soil temp.	0.61_{12}**
Chase *Myotis*	Ave. temp. (in wood) (-ve)	$8.0_{1,8}$**	Ave. temp. " " Suction trap	Suction trap Light trap Sweep net Ave. temp.	-0.83_{10}*** -0.59_{10}* -0.72_{10}** 0.61_{10}*
Long Itch *P. pip.*	Max. temp. (+ve)	$11.5_{1,11}$***	Sweep net	Max. temp.	0.57_{13}*
Long Itch *Myotis*	No predictors	n/a	No sign. corr. (Pearson correlation)	n/a	n/a

6.3.1.2.2 Roughknowles Wood

- Regression

  P. pipistrellus activity was predicted by barometric pressure (+ve).

  No weather variables were significantly regressed against *Myotis* spp. activity (Table 6.4).

- Multiple partial correlation

  Average *P. pipistrellus* activity along the whole transect was significantly correlated with pressure (+ve) with either suction trap or light trap numbers held constant. With barometric pressure held constant, activity was correlated to the number of insects caught in the sweep net. This suggests that barometric pressure may be a less significant regulator of pipistrelle activity than sweep net sample numbers.

  Sweep net numbers were highly correlated with *Myotis* spp. activity , more so than with suction trap or light trap numbers (n=9, r=0.16 and r=-0.15 respectively). (Table 6.4).

6.3.1.2.3 Chase Wood

- Regression

  In Chase Wood soil temperature (+ve) best described variations in *P. pipistrellus* activity along the transect each night.

  The most significant predictor for *Myotis* spp. activity was average temperature (+ve).

- Multiple partial correlation

  With the effects of insect numbers caught in the sweep net, light trap or suction trap held constant soil temperature was not significantly correlated with pipistrelle activity. The number of insects caught in the suction trap was significantly correlated with pipistrelle activity while soil temperature was held constant.

From multiple partial correlation *Myotis* spp. activity along the whole transect in Chase Wood was negatively correlated with average temperature while insect trap numbers were held constant. A significant association was also found between suction trap numbers and activity with temperature held constant (Table 6.4).

6.3.1.2.4 Long Itchington

- Regression

  P. pipistrellus activity along the Long Itchington Wood transect was most accurately predicted by maximum temperature (+ve).

  No significant predictors were found for *Myotis* spp. activity.

- Multiple partial correlation

  Activity of pipistrelles was significantly correlated with sweep net numbers while maximum temperature was held constant.

  Using Pearson correlation none of the insect sample numbers were significantly correlated with *Myotis* spp. activity (Table 6.4).

6.3.2 P. pipistrellus *and* Myotis *spp. activity and insect abundance related to different weather variables in different microhabitats*

Fewer accurate predictors were found for *Myotis* activity in different microhabitats than for *P. pipistrellus*. This may be a function of smaller sample sizes for *Myotis* spp.

6.3.2.1 Pipistrellus pipistrellus

Weather variables were found to accurately predict pipistrelle activity in 19 out of 22 microhabitats using multiple regression analysis. Temperature was the most accurate variable determining activity in many (10 microhabitats out of 19). The other variables found to predict pipistrelle activity were barometric pressure (6 microhabitats), relative humidity (5), and

sunlight hours (2). Maximum temperature, soil temperature and minimum temperature were all positively related to activity.

From correlation analysis (multiple partial or Pearson's), pipistrelle activity in 13 microhabitats out of 22 was found to correlate significantly either with insect abundance, or, with a weather variable while insect numbers were held constant (from both sweep net and suction trap; light trap numbers were not included in multiple partial correlation analysis of microhabitat activity).

Temperature was the correlated variable in only 4 of the 13. Eight were correlated significantly with insect numbers either from the sweep net or suction trap. Barometric pressure was a significant correlate in two microhabitats only. Humidity was not significantly correlated with activity in any microhabitats. These results suggest that humidity indirectly affects pipistrelle activity by affecting insect abundance (Tables 6.5-6.8).

Table 6.5 **Bat activity with correlated variables from regression and correlation analysis, Tocil Wood microhabitats.**

Microhabitat/ species (Y)	Regressed (X) variables	F-value$_{df}$	Multiple partial correlation (or Pearson): Significant correlate	Variable held constant	r value$_n$
Dense vegetation 1 *P. pipistrellus*	Min. temp. (+ve)	$29.8_{1,10}$ ***	Suction	Min. temp.	0.59_{12}*
Dense vegetation 1 *Myotis* spp.	Windspeed (+ve)	$7.28_{1,8}$*	Windspeed	Suction Sweep	0.64_{10}* 0.70_{10}*
Dense vegetation 2 *P. pipistrellus*	No predictors	n/a	Suction (Pearson correlation)	n/a	0.6212*
Dense vegetation 2 *Myotis* spp.	Rel. humidity (-ve)	$18.78_{1,8}$ ***	Rel. humidity	Suction Sweep	-0.83_{10}*** -0.85_{10}***
Edge *P. pipistrellus*	Min. temp. (+ve)	$7.62_{1,11}$ **	Sweep	Min. temp.	0.62_{13}**
Edge *Myotis* spp.	Windspeed (+ve)	$7.09_{1,9}$**	Windspeed	Suction Sweep	0.69_{11}** 0.67_{11}**
Natural glade *P. pipistrellus*	Min. temp. (in woodland) (+ve) and Bar. pressure (-ve)	$8.88_{2,10}$ ***	Bar. pressure	Min. temp. and suction Min. temp. and sweep	-0.55_{13}* -0.59_{13}*
Natural glade *Myotis* spp.	No predictors	n/a	Suction (Pearson correlation)	n/a	0.54_{10}*
Path *P. pipistrellus*	Min. temp. (+ve)	$30.8_{1,11}$ ***	Min. temp. " Suction	Suction Sweep Min. temp.	0.62_{13}** 0.75_{13}*** 0.57_{13}*
Path *Myotis* spp.	Sunlight hrs (-ve)	$7.77_{1,9}$**	Sunlight hrs.	Suction Sweep	-0.70_{11}** -0.69_{11}**
Woodland *P. pipistrellus*	Sunlight hrs (-ve) & Rel. humid.(in woodland) (+ve)	$6.06_{2,9}$**	No sign. correlations with suction included	n/a	n/a
Woodland *Myotis* spp.	Sunlight hrs (-ve)	$5.03_{1,8}$*	No sign. correlations with sweep net included	n/a	n/a

Table 6.6 **Bat activity with correlated variables from regression and correlation analysis, Roughknowles Wood microhabitats.**

Microhabitat/ species (Y)	Regressed (X) variables	F-valuedf	Multiple partial correlation (or Pearson): Significant correlate	Variable held constant	r value$_n$
Dense vegetation *P. pipistrellus*	Sunlight hrs (-ve)	$4.11_{1,8}$*	Suction	Sunlight hrs.	0.61_{10}*
Dense vegetation *Myotis* spp.	Insufficient data	n/a	Insufficient data	n/a	n/a
Edge *P. pipistrellus*	Bar. pressure (+ve)	$4.85_{1,10}$ **	Sweep	Bar. pressure	0.66_{12}**
Edge *Myotis* spp.	Insufficient data	n/a	Insufficient data	n/a	n/a
Open woodland 1 *P. pipistrellus*	Bar. pressure (+ve)	$6.71_{1,10}$ **	Sweep	Bar. pressure	0.81_{12} ***
Open woodland 1 *Myotis* spp.	Bar. pressure (+ve)	$5.9_{1,10}$**	Sweep	Bar. pressure	0.73_{12}**
Open woodland 2 *P. pipistrellus*	Bar. pressure (+ve)	$7.49_{1,8}$**	Bar. pressure	Sweep Suction	0.69_{10}** 0.69_{10}**
Open woodland 2 *Myotis* spp.	Insufficient data	n/a	Insufficient data	n/a	n/a

Table 6.7 **Bat activity with correlated variables from regression and correlation analysis, Chase Wood microhabitats.**

Microhabitat/ species (Y)	Regressed (X) variables	F-ratio$_{df}$	Multiple partial correlation (or Pearson): Significant correlate	Variable held constant	r value$_n$
Clear-cut *P. pipistrellus*	Soil temp. (+ve)	$12.5_{1,10}$ ***	Soil temp.	Sweep	0.74_{12}***
			"	Suction	0.81_{12}***
Clear-cut *Myotis* spp..	No predictors	n/a	Suction (Pearson correlation)	n/a	0.59_{10}*
Dense vegetation *P. pipistrellus*	Rel. humid. (-ve)	$4.7_{1,10}$*	No sign. correlations with suction included	n/a	n/a
Dense vegetation *Myotis* spp..	Min. temp. (in woodland) (-ve)	$6.3_{1,8}$**	No sign. correlations with suction or sweep incl.	n/a	n/a
Edge *P. pipistrellus*	Soil temp. (+ve)	$4.8_{1,10}$*	No sign. correlations with suction included	n/a	n/a
Edge *Myotis* spp..	Rel. humid. (in woodland) (+ve)	$4.4_{1,8}$*	*No sign. correlations with* suction or sweep incl.	*n/a*	*n/a*
Natural glade *P. pipistrellus*	Rel. humid. (-ve) and Bar. press. (-ve)	$6.6_{1,10}$ **	No sign. correlations with suction included	n/a	n/a
Natural glade *Myotis* spp..	Rel. humid. (ve)	$5.4_{1,9}$**	Sweep	Rel. humidity	0.77_{11}***
Woodland *P. pipistrellus*	Rel. humid. (-ve)	$5.9_{1,10}$ **	No sign. correlations with suction or sweep incl.	n/a	n/a
Woodland *Myotis* spp..	No predictors	n/a	Sweep (Pearson correlation)		0.55_{11}*
Open woodland *P. pipistrellus*	Rel. humid. (-ve) and Bar. press. (-ve)	$4.4_{1,10}$ **	Sweep	Rel. humid. & Bar. press.	0.62_{12}**
Open woodland *Myotis* spp..	No predictors	n/a	No sign. correlations with sweep or suction	n/a	n/a

Table 6.8 **Bat activity with correlated variables from regression and correlation analysis, Long Itchington Wood microhabitats.**

Microhabitat/ species (Y)	Regressed (X) variables	F-ratio$_{df}$	Multiple partial correlation (or Pearson): Significant correlate	Variable held constant	r value$_n$
Clear-cut	Max. temp. (+ve)	$59.5_{1,10}$ ***	Max. temp.	Suction	0.76_{12}***
P.pipistrellus				Sweep	0.81_{12}***
Clear-cut	Windspeed (+ve)	$5.32_{1,8}$*	Windspeed	Suction	0.64_{10}*
Myotis spp..				Sweep	0.66_{10}**
Dense vegetation	No predictors	n/a	No sign. correlations with suction or sweep	n/a	n/a
P.pipistrellus					
Dense vegetation	Windspeed (-ve)	$4.09_{1,8}$*	Windspeed	Suction	-0.63_{10}*
Myotis spp..				Sweep	-0.58_{10}*
Edge	Max. temp. (+ve)	$9.26_{1,10}$ **	No sign. correlations with suction included	n/a	n/a
P.pipistrellus					
Edge	Bar. pressure (-ve)	$4.09_{1,8}$*	No sign. correlation with suction included	n/a	n/a
Myotis spp..					
Ride	Max. temp. (+ve)	$9.44_{1,10}$ **	No sign. correlations with suction or sweep incl.	n/a	n/a
P.pipistrellus					
Ride	No predictor	n/a	No sign. correlations with suction or sweep	n/a	n/a
Myotis spp..					
Woodland 1	No predictor	n/a	No sign. correlations with suction or sweep	n/a	n/a
P.pipistrellus					
Woodland 1	No predictor	n/a	Sweep (Pearson correlation)	n/a	0.73**
Myotis spp..					
Woodland 2	Max. temp. (+ve)	$6.93_{1,10}$ **	Max. temp.	Suction	053_{12}*
P.pipistrellus				Sweep	0.54_{12}*
Woodland 2	Sunlight hrs (-ve)	$6.41_{1,6}$*	No sign. correlations with suction included	n/a	n/a
Myotis spp..					

6.3.2.2 Myotis *spp.*

Weather variables accurately predicting *Myotis* spp. activity from regression were found in 13 microhabitats out of 22. Weather variables significantly regressed against activity were: windspeed (4 microhabitats), humidity (3), sunlight hours (3), barometric pressure (2), and minimum temperature (1).

Significant correlations with activity were also found in 13 microhabitats with either weather variables or insect numbers held constant (multiple partial correlation) or insect numbers alone correlated (Pearson correlation). In six of these, insect numbers were the significant correlates. Windspeed (4), sunshine (2) and humidity (1) were also associated with activity (Tables 6.5-6.8).

6.3.2.3 Sweep netted insects

In 18 out of 22 microhabitats, sweep netted insect abundance was accurately predicted by one or two weather variables. Temperature (7 microhabitats), and relative humidity (6) were both important predictors of sweep netted insect abundance. Several other variables were significantly regressed. These were: pressure (1), windspeed (2), rainfall (1), and cloud cover (2) (Table 6.9).

Table 6.9 **Sweep netted insect abundance in different microhabitats regressed against weather variables**

Microhabitat	Woodland	Regressed (X) variable	F-ratio$_{df}$
Natural glade	Tocil	Sunlight hrs. (-ve)	$5.5_{1,10}$**
	Chase	Rel. humidity (-ve)	$29.8_{1,10}$***
Clear-cut glade	Chase	Rel. humidity (-ve)	$9.7_{1,10}$***
	Long Itch	Max. temp.	$19.3_{1,11}$***
Open woodland	Rough 1	Soil temp. (+ve)	$6.4_{1,11}$**
	Rough 2	Min. temp. (+ve)	$12.5_{1,11}$***
	Chase	Rel. humidity (-ve)	$13.8_{1,10}$***
Woodland	Tocil	Cloud cover (in woodland) (-ve)	$6.7_{1,11}$**
	Chase	No predictors	n/a
	Long Itch 1	Soil temp. (+ve) & Rainfall (-ve)	$5.3_{2,9}$**
	Long Itch 2	No predictors	n/a
Ride	Tocil	Min. temp. (+ve)	$6.7_{1,10}$**
	Long Itch	Cloud cover (+ve)	$6.9_{1,10}$**
Dense vegetation	Tocil 1	Min. temp. (+ve)	$12.7_{1,10}$***
	Tocil 2	No predictor	n/a
	Rough	Windspeed (-ve) & Bar. pressure (+ve)	$11.6_{2,10}$***
	Chase	Rel. humidity (-ve)	$16.9_{1,10}$***
	Long Itch	Sunlight hrs. (+ve)	$10.4_{1,10}$***
Edge	Tocil	Soil temp. (+ve) & Rel. humidity (-ve)	$7.4_{2,10}$***
	Rough	Windspeed (-ve)	$5.6_{1,11}$**
	Chase	Rel. humidity (-ve)	$4.3_{1,10}$*
	Long Itch	No predictors	n/a

6.3.3 Summary of 1995 results

Climatic regressor variables were not specific to microhabitat types (e.g. edges or natural glades). These results do not confirm the findings of Walsh and Mayle (1991), that minimum temperature is important in habitats of high activity but not in areas of low activity levels.

A comparison of predictors for *Myotis* spp. activity, pipistrelle activity and insect abundance, in woodland microhabitats, shows interesting results.

Temperature may be less important to *Myotis* spp. than to pipistrelles because temperature was found to be significantly correlated in only one microhabitat for *Myotis* spp. compared with 10 microhabitats for *P. pipistrellus*. Windspeed may be less important to *P. pipistrellus* than *Myotis* spp. because it was significantly regressed in four different microhabitats for *Myotis* compared with none for *P. pipistrellus*.

From regression analysis, relative humidity was a significant predictor of both pipistrelle activity and insect abundance in a similar number of microhabitats (5 and 6 respectively). However, using multiple partial correlation with pipistrelle activity, relative humidity was not a significant correlate in any microhabitat once the effects of insect numbers had been allowed for.

Certain variables were more important in particular woodlands. In Long Itchington Wood, maximum temperature was the most commonly correlated variable, in Roughknowles windspeed and barometric pressure were important and relative humidity in Chase Wood.

6.3.4 1995 and 1996

P. pipistrellus pass data in each microhabitat of Chase Wood, 1996, were correlated against weather variables. Multiple partial correlation was used to keep the effects of the lunar cycle constant while analysing the effects of climate.

Although bat activity was estimated differently in the two years, there is opportunity to make comparisons. Observations on activity in 1996 were made after dusk emergence so it would be inappropriate to compare overall bat activity from a full night of transect walking in 1995 with the results from 1996. Instead, data from the first transects covered each night (around dusk) in Chase Wood were used. With this data (no. of *P. pipistrellus* passes per 100m of first transect) regression analyses were conducted to obtain significant predictors for both overall transect and individual microhabitats. In 1995, the most significant predictor of first transect *P. pipistrellus* activity was minimum temperature (+ve) ($F=8.03_{df1,10}$, $p<0.05$).

Microhabitats were examined individually. Minimum temperature in 1995 (first transect) was found to be important with a significant ($p<0.1$) positive relationship found between it and *P. pipistrellus* activity in four out of the six microhabitats studied in Chase Wood (Table 6.10).

Overall pipistrelle activity in Chase Wood, 1996 was not significantly correlated with any climate variables. In three of the six microhabitats *P. pipistrellus* activity was found to significantly correlate with climate variables (with effects of the lunar cycle held constant). In the woodland microhabitat, minimum temperature at grass level (-ve), sunlight hours (+ve) and humidity (-ve) were the most significantly correlated variables. Minimum temperature was significantly negatively correlated with activity in the open woodland microhabitat. At the edge, pipistrelle activity was negatively related to hours of sunshine. Three of the six microhabitats were not found to have any significant predictors for activity in 1996 (Table 6.10).

Table 6.10 **Weather variables significantly correlated with pipistrelle activity in Chase Wood, 1995 and 1996**

Microhabitat	1995 predictor variable	F-value (df1,10)	1996 correlated variables (lunar cycle constant)	r-value (n=10)
Natural glade	Min. temp. (+ve)	4.6*	No sign. correlated variables	n/a
Clear-cut	Min. temp. (+ve)	5.2**	No. sign. correlated variables	n/a
Open Woodland	Soil temp. (+ve)	4.3*	Min. temp. Grass temp.	-0.59* -0.60*
Woodland	Min. temp. (+ve)	4.6*	Min. temp Grass temp. Sunshine hours Rel. humidity	-0.67** -0.70** 0.66* -0.65*
Dense vegetation	Insufficient data	n/a	No sign. correlated variables	n/a
Edge	No predictor	n/a	Sunshine hours	-0.67**

6.4 Discussion

6.4.1 Temperature

Minimum flight temperatures for nocturnal insects were noted by Wellington (1945) to range from 1.1°C to 13.9°C in laboratory conditions. Peng (1991) in his study of dipterans found that different family abundances could be predicted by different variables. Some families such as Phoridae and Tipulidae remain active in warm conditions. Rautenbach *et al.* (1988) in their study of arthropod availability and bat abundance in South Africa found that the combination of highest daily relative humidity and the highest night-time temperature, immediately after sunset, created conditions most favourable for

arthropod flight activity resulting in the brief peak of availability of aerial arthropods at dusk.

By affecting the numbers of insects present, temperature has a knock-on effect on bat activity. However, the influence of temperature on bat activity is not solely indirect. Bats themselves may have minimum flight temperatures and are known to fly for shorter periods on cool nights (see section 6.1.1).

When *P. pipistrellus* activity data (along whole transect) from all four woodlands taken together (1995) were regressed against weather variables, the climate factor found to best predict activity was soil temperature (from Bablake Weather Station). The relationship was positive. With data from all four woodlands combined, soil temperature also best predicted the number of insects caught in the suction trap. From the results of multiple partial correlation when insect numbers are held constant, soil temperature does not appear to retain a direct effect on pipistrelle activity.

In three out of the four woodlands, when analysed individually, insect abundance was related positively to temperature. Temperature was the most accurate predictor of pipistrelle activity along the whole transect in the same three woodlands. However, the effect of temperature on activity in each woodland seemed to diminish when either sweep net or suction trap catch numbers were held constant in multiple partial correlation. This suggests that overall pipistrelle activity in each woodland is a function, at least partly (if statistically insignificant), of insect availability and not temperature alone.

In fewer than 33% (7) of individual microhabitats studied, temperature was a predictor of sweep netted insect abundance. Temperature played an important role regulating pipistrelle activity in almost 50% (10) of microhabitats, according to regression analysis results. *P. pipistrellus* activity

was influenced by temperature in four out of the six microhabitats examined in each of Long Itchington Wood and Tocil Wood.

When insect numbers were included in multiple partial correlation analyses, temperature became a less dominant correlate, and was significantly associated with pipistrelle activity in 4 microhabitats only, while insect abundance was significantly correlated with activity in 8 microhabitats.

This shows that overall pipistrelle activity as well as pipistrelle activity within each woodland may be indirectly affected by temperature through insect availability, i.e. temperature (during the active summer season) may be more important as a regulator of insect availability than as a factor directly influencing pipistrelle activity. Rautenbach *et al.* (1988) noted that the effects of temperature on insect availability may indirectly affect bat activity.

Different measurements of temperature were taken during the study; maximum, minimum and soil temperature from Bablake and night time average, maximum and minimum from each woodland. In Long Itchington Wood, maximum temperature from Bablake was often the regressor variable while in Tocil Wood minimum temperature, also from Bablake, was often the predictor variable in microhabitats. Possible reasons why different temperature measurements correlated predominantly in different woodlands are discussed in greater detail below (section 6.4.7).

Relative activity of *Myotis* spp. appears to be less predictable using temperature variables than *P. pipistrellus* activity. Overall *Myotis* spp. activity was predicted by a combined negative relationship with relative humidity and barometric pressure.

6.4.2 Humidity

Although Wellington (1945) found that changes in relative humidity seemed to have little effect upon insects, Peng (1991) found that many

dipteran families preferred dry conditions for flight. These included the Ceratopogonidae and Chironomidae (both of which were present in trap samples in this study, see Tables 5.3-5.5). Low windspeed and dry conditions are also important to some night flying dipterans such as Psychodidae and Cecidomyiidae (also present in trap samples, see Tables 5.3-5.5).

Overall pipistrelle activity and insect trap numbers in all four woodlands taken together were not found to be significantly correlated with humidity. However, *Myotis* spp. activity from all four woodlands combined was significantly predicted by a combined negative relationship with humidity and pressure. Upon further analysis, humidity was not significantly correlated with *Myotis* spp. activity when the effects of pressure and sweep netted insect numbers were held constant.

Pipistrelle and *Myotis* spp. activity in individual woodlands were not significantly predicted by humidity. However, humidity was accurately related to pipistrelle activity in 5 microhabitats and to *Myotis* spp. activity in 3. It was also correlated to sweep netted insect abundance in 6 microhabitats. From multiple partial correlation of bat activity in microhabitats (with insect numbers held constant) humidity was not significantly correlated with pipistrelle activity in any microhabitats and with *Myotis* spp. activity in 1 microhabitat only. This suggests that humidity is important to bat activity only through its influence on insect abundance.

In all cases in this study, where relative humidity was found to be a significant predictor of sweep netted insect abundance, the relationships were negative i.e. insects preferred dry conditions.

The negative link between humidity and pipistrelle activity from regression contrasts with the findings of Adam *et al.* (1994) where bat activity declined with lower relative humidity. Adam *et al.* suggested that high relative humidity may be important to bats in order to minimise water loss.

However, woodlands often have a more humid microclimate than exposed habitats (Neal, 1958) so it is possible that relative humidity was important to active bats only by influencing insect prey abundance.

In Chase Wood where relative humidity (from Bablake) was significantly negatively related to *P. pipistrellus* activity in four out of the six microhabitats studied, humidity was also significantly negatively correlated with maximum temperature and soil temperature (from Bablake) during those study nights. In Chase Wood, therefore, the negative correlations between bat activity and insect abundance with humidity may be related to temperature.

Adam *et al.* (1994) suggested that bats prefer high humidity, and in Chapter 4 it was suggested that in dry summers bats may use internal woodland microhabitats more than exposed microhabitats. If this was the case then it may have been expected for bat activity at edges, in 1995, to be positively correlated with humidity but negatively correlated in internal microhabitats, or, for bat activity at edges to be negatively related to temperature and positively related to temperature in internal microhabitats. Data did not show much evidence to prove this hypothesis except for *Myotis* spp. passes in Chase Wood in 1995. Activity at the edge was positively correlated with humidity (despite a negative relationship between insect abundance and humidity) while activity in other microhabitats in the same woodland was negatively correlated with humidity. However, this occurred in one of the woodlands only and no firm conclusions can be drawn.

6.4.3 Barometric Pressure

There is little conclusive evidence showing that barometric pressure has any effect upon insect abundance. Wellington (1945) noted an increase in flight activity among Diptera and Coleoptera within the pressure range between sea level and a height of about 1.5km. This is likely to affect vertical

distribution but not distribution immediately above ground level in the study area.

Some authors have observed variations in insect activity with changing pressure. Underhill (1940) noted Simuliidae feeding more readily during low or falling pressure levels. Parman (1920) observed fewer Diptera when air pressure dropped before a severe storm.

Bats may sense barometric pressure using the paratympanic organ (Vitali organ) (Paige, 1995). Bats are the only mammal known to possess it and it is likely that pressure measurement is its function (Griffin, 1969; Jorgensen, 1984; Von Bartheld & Rubel, 1989). Paige (1995) suggested that barometric pressure tracking may allow cave dwelling bats to make predictions regarding insect abundance. Paige found a negative relationship between insects and barometric pressure and also between bat activity and pressure.

Despite the fact that Paige (1995) found a negative association between insect abundance and barometric pressure, many of the evening and night flying dipterans prefer calm and dry conditions (Peng, 1991). These conditions are particularly associated with high air pressure masses (anti-cyclones) during the British summer season (Taylor and Yates, 1967). High air pressure masses were present during much of the summer of 1995. There was a significant correlation between humidity (measured in woodlands) and barometric pressure (see Appendix II, Table II.i). The correlation was negative so high air pressure probably resulted in dry conditions in 1995. However, there was no significant direct correlation between total insect abundance measured in any of the three traps (all four woodlands combined) and barometric pressure.

In this study, overall pipistrelle activity from all four woodlands combined was not significantly correlated with barometric pressure. *Myotis*

spp. activity from all four woodlands combined was, however, negatively related to pressure. This association remained significant even when multiple partial correlation was carried out with insect numbers held constant. The correlation between *Myotis* spp. activity and barometric pressure was negative and this concurs with Paige's results of higher bat activity during low pressure instances.

P. pipistrellus activity along the whole transect in Roughknowles Wood was positively associated with barometric pressure (regression). However, when multiple partial correlation was carried out, holding sweep netted insect numbers constant, pressure was not significantly correlated with activity.

In Roughknowles Wood, the overall number of insects caught in the sweep net was significantly positively related to pressure and negatively to windspeed. Insects could easily be blown away by wind in Roughknowles Wood. It is vulnerable to wind because it is situated on a small hill (100m above sea level) and has recently been thinned. Little shelter is provided by the few remaining trees. Insect emergence in Roughknowles Wood may have been associated with dry, high pressure events and this could have resulted in the positive relationship between bat activity and barometric pressure. In Roughknowles Wood, pressure was not significantly correlated with any other variables except the number of insects caught in the sweep net (see Appendix II, Table II.iii).

P. pipistrellus activity and barometric pressure were found to be related (multiple regression) in six microhabitats, while sweep netted insect abundance was only significantly associated with barometric pressure in one microhabitat. *Myotis* spp. activity was correlated with pressure in two microhabitats (multiple regression). The relationship between pipistrelles and pressure was negative in three microhabitats and between *Myotis* spp. and

pressure in one. Four positive occurrences (3 pipistrelle, 1 *Myotis* spp.) were all located in Roughknowles Wood. From multiple partial correlation, pressure remained a significant correlate with pipistrelle activity (with insect numbers held constant) in two microhabitats, one in Roughknowles Wood (+ve) and one in Tocil Wood (-ve).

Paige (1995) stated that when pressure is low, insects are most abundant, except during heavy rainfall. In this study, no significant relationship was found between pressure and insect abundance (all four woodlands combined) and the r coefficient, although insignificant, was positive (between suction trap or sweep net numbers and pressure). Therefore, the negative association in some microhabitats, between bat activity and barometric pressure, is unlikely to indicate that bats were availing of high associated insect abundance.

However, in a Tocil Wood microhabitat where a significant relationship between pipistrelle activity and barometric pressure remained even after insect numbers had been accounted for, pressure was significantly and negatively correlated with relative humidity and minimum temperature (see Appendix II, Table II.ii).

The negative link between overall *Myotis* spp. activity and activity of pipistrelles in certain microhabitats with barometric pressure, independently of links with insect abundance, points toward barometric pressure directly affecting activity.

6.4.4 Windspeed

Windspeed was important to the flight activity of many insects in Peng's (1991) study, especially at dusk with some of the weak flying dipterans preferring calm conditions. Tipulidae (even though tipulids are relatively large they are poor flyers (Service, 1973b)), Ceratopogonidae and

Chironomidae select calm conditions. The activity of small body sized Phoridae was enhanced in sheltered conditions while big bodied Anisopodidae showed greater activity in exposed conditions (Peng, 1991).

Overall activity of *Myotis* spp. or pipistrelles in all four woodlands combined, or in woodlands analysed separately, was not significantly associated with windspeed.

Insect abundance was related to windspeed (-ve) in one woodland (Roughknowles). However, bat activity in Roughknowles was not significantly correlated with windspeed either along the whole transect or in microhabitats.

A significant relationship was found from regression analysis between windspeed and *Myotis* spp. activity in four microhabitats. The two woods where *Myotis* spp. activity was related to windspeed were Long Itchington and Tocil Wood. The relationship from regression analysis was negative in one dense vegetation microhabitat (Long Itchington), and positive in two open microhabitats (edge, Tocil and clear-cut, Long Itchington) and one dense vegetation microhabitat (Tocil). These relationships remained significant even when insect numbers were held constant as part of multiple partial correlation analysis.

The phenomenon of aerial insect build up on the lee side of windbreaks has been mentioned in Chapter 4. The edge studied in Tocil Wood was on the north-east side of the woodland, however, another windbreak (of tall trees) exists less than 50m to the north of this edge. Insects probably build up in the meadow in between during both North-Easterly and South-Westerly wind instances and these were the two predominant wind directions from April to September, 1995 (BWS). A significant correlation was found between insect numbers caught in the sweep net at the edge and windspeed (see Appendix II, Table II.ii). However, a similar accumulation of insects did not occur in the clear-cut of Long Itchington Wood where no

relationship was found between windspeed and insect numbers from the sweep net (Appendix II, Table II.v).

A significant association between windspeed and *Myotis* spp. activity was found in two densely vegetated microhabitats. In Tocil Wood, the relationship was positive and in Long Itchington the relationship was negative. In both of these microhabitats the relationships between insect abundance and windspeed were not significant. This contrast in the nature of the relationships may have foundation in where the two woodlands are situated. Tocil Wood is situated in a small valley and may be less prone to wind than Long Itchington (on a hill). During high winds bats may move into Tocil Wood whereas in Long Itchington Wood it may benefit bats to move into sheltered clear-cuts.

6.4.5 Other climate variables affecting insect or bat abundance

The negative association between activity of some species of bat (e.g. *P. auritus* Entwistle *et al.*, 1996) and rainfall was not observed in this study. This may have been attributable to the particularly low rainfall during 1995. However, insect abundance in sweep nets (from all four woodlands) was negatively associated with rainfall.

Cloud cover and hours of sunshine were seldom significantly regressed against insect or bat activity in microhabitats. This suggests that these variables were not important in regulating the activity of bats or insect availability. Where sunlight hours were significantly linked with bat activity, the relationship was usually negative. This finding is difficult to explain and may have some background in bats roosting within the woodland itself.

6.4.6 Weather variables and insects influencing bat activity

From the results of regression analysis followed by multiple partial correlation, many of the seemingly direct relationships between bat activity

and weather fluctuations can be described in terms of varying insect availability. This was certainly the case where temperature and humidity were correlated with bat activity.

Temperature was less often significantly correlated with *Myotis* spp. activity than with *P. pipistrellus* activity. This may be the result of different foraging strategies used by the two groups. *P. pipistrellus* relies almost completely upon aerial insects while the *Myotis* spp. probably include gleaned prey in their diet. As a result, temperature, which has a direct effect on aerial insect abundance is less important to *Myotis* spp.

Windspeed and barometric pressure may directly influence bat activity, although the extent to which they do so may be a function of site features.

6.4.7 Variables in different woodlands

In Tocil Wood, minimum temperature was the climate variable most often correlated with bat and insect abundance. This may be because the woodland is in a small valley and dense cool air falls quickly onto the valley floor during the night. As a result, minimum temperature regulates the abundance of insects and perhaps to some extent bat activity (more so than maximum daytime temperatures for example) more extensively than in a woodland situated on top of, or at the side of, a hill.

Windspeed was one of the variables most often correlated with insect abundance in Roughknowles. This is understandable because the site is unsheltered. Barometric pressure was also correlated with bat and insect abundance suggesting that dry, high pressure conditions encouraged the emergence of insects there.

In Long Itchington Wood, maximum temperature played a more important role than in any other woodland. A possible reason for this is the canopy density. There are very few natural openings in the canopy in Long

Itchington Wood and, as a result, high temperatures may be required to heat up the ground and precipitate insect emergences.

In Chase Wood, relative humidity was important to bats (without insects held constant) and to sweep netted insects.

6.4.8 Microhabitat types and patterns to predictor weather variables

There do not appear to be any patterns to the types of weather variables useful for predicting insect or bat activity in different microhabitats. Significantly correlated weather variables seem to be a function, at least partly, of site features and overall situation. More work needs to be done on this to verify that weather variables predicting bat or insect activity are not specifically common to certain microhabitat types.

6.4.9 1996 and 1995

The lack of significantly correlated variables from 1996 data may have been a result of the different methods used for estimating activity (although, see section 7.3.6). However, there is also the possibility that weather conditions may have influenced bat distribution during 1996 in a different way than during 1995.

The summer of 1995 was the hottest recorded in the area (records date from 1892) and rainfall dropped to 73% below the thirty year average. Despite the relative warmth of the two summer months of June and July 1996, the average temperature for 1996 up until then was 0.4°C below average. June 1996 was the wettest one since 1993 and although July was relatively dry, rainfall was only 33% below average.

Weather may have correlated less with activity in 1996 than in 1995 because the wetter summer may have resulted in bats relying less on the humid woodland microclimate as all habitats were more humid in 1996 than in 1995.

In 1996, where internal microhabitat activity was correlated with temperature, the relationship was negative: as minimum temperature increased, bat activity decreased. Sunshine hours and activity in the woodland microhabitat correlated positively, contrasting with sunshine and activity correlations in 1995. The relationship with humidity was negative.

In contrast to 1995, in 1996, bats were present during cooler nights and were less active in the woodland during warmer nights. Kindvall (1995) noted that habitat use changes may occur with climate changes and this appears to be supported by the limited data available in 1996, however, more research needs to be conducted.

Summary

Temperature was correlated with activity in woodland microhabitats regardless of whether microhabitats were selected by bats or not. Temperature was found to significantly correlate with *P. pipistrellus* activity, but less so with *Myotis* spp. activity. Correlations between bat activity and temperature probably reflect the influence of temperature on prey availability. Humidity was generally negatively correlated with bat activity, therefore bats were not avoiding activity during periods of low humidity to prevent excess water loss. Overall, windspeed appeared to have little effect on bat activity although its effects are probably very localised.

Chapter 7

THE RELATIONSHIP BETWEEN BAT PASSES AND BAT DENSITY: A COMPUTER SIMULATION

7.1 Introduction

The relationship between measured bat passes and bat density is unknown. Thomas and La Val (1988) claimed that there is likely to be no connection between the two. This chapter examines the association using a two-dimensional computer model. Many local and national studies use bat passes as an index of activity, however it is unknown whether high activity measurements are a reflection of high bat numbers. The model simulates observation of bats by a human observer using a bat detector in a known area. Its outputs are the number of recorded bat passes and the density of bats.

The simulation describes a woodland (square or rectangular) in which a known number of bats are randomly placed. The bats move around the woodland at a constant speed. An observer is located within the woodland and measures the number of bat passes, either while moving along a line transect or from a stationary position.

7.2 Model description

7.2.1 Structure and setup

7.2.1.1 Structure of the model

Basic structure of the model can be seen in Fig 7.1. Firstly, variables and arrays used in the model are set up. A model wood is defined, bats are distributed randomly throughout and the observer is placed within. The positions of the bats relative to the observer are checked and bat passes recorded if appropriate. Next, the bats are moved, followed by the observer (where appropriate).

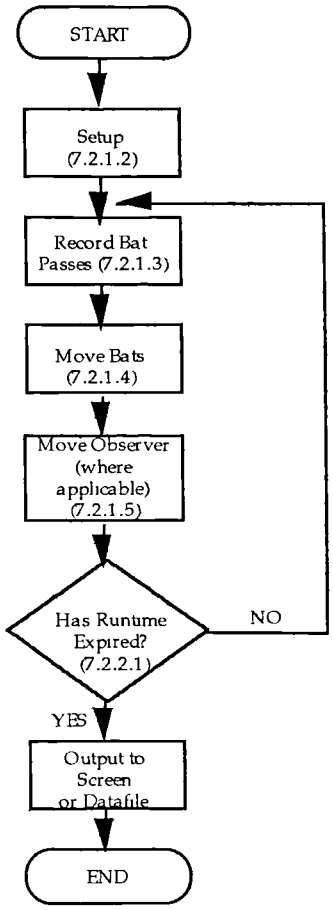


Fig 7.1 Flowchart describing the basic structure of Batmodels

The checking process is carried out again, then the bats (and observer) are moved and the whole process is iterated for a certain length of time. Recorded bat passes and density of bats are outputted to the screen or to a datafile.

7.2.1.2 Setup

The wood can be envisaged as a rectangular plane with one corner at the origin. It is given a constant length and width by the model. The observer is at a point in the centre of the wood in the case where the observer is stationary, and close to one end of the wood in the case where the observer moves. A matrix with the number of rows equal to the number of bats is set up. Each row contains coordinates for a bat, and flags indicating whether the bat is in observation range and was in observation range at the last iteration. Before

the first iteration, each bat is randomly assigned coordinates within the wood. Physical variables such as bat flight speed are also given values at this stage (choice of particular values is discussed in section 7.2.2).

7.2.1.3 Recording bat passes

How bat passes are recorded depends on how many bats are in observation range (see section 2.3.2). Modelling of the recording of bat passes is based on the assumption that it is not possible to distinguish more than two bats simultaneously.

If no bats are in observation range

- a single bat coming into range is recorded as one bat pass
- two bats simultaneously coming into range is recorded as two bat passes
- more than two bats entering observation range simultaneously is recorded as two bat passes, as only the two closest to the observer are recorded

If there is one bat already in observation range

- one or more than one new bat(s) coming into range is recorded as one bat pass

If there is more than one bat already in observation range

- if the closest bat was neither the closest nor the second closest last iteration, one bat pass is recorded
- **otherwise** if the second closest bat was neither the closest nor the second closest last iteration, one bat pass is recorded

Note that if there is more than one bat in observation range only one bat pass at a time can be recorded. This mirrors reality because the human ear cannot distinguish several echolocating bats and the loudest stream of echolocation pulses is recorded as a bat pass. As a consequence the maximum number of recorded bat passes will be equal to the number of iterations of the model.

7.2.1.4 Moving the bats

Bat movement was modelled in two different ways. In one version of the model, bats moved in circles at a constant speed. In another, bats moved at a constant speed with the direction of motion changing at random every iteration. Bats were constrained to flying within the boundaries of the wood in order to keep their density constant (Fig 7.2).

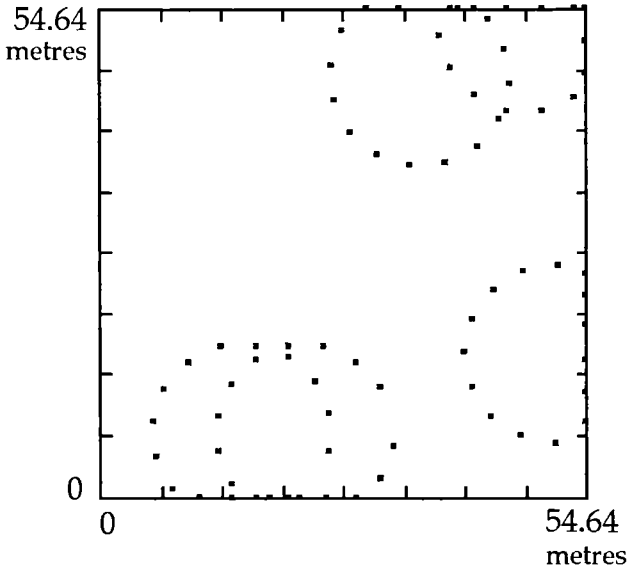


Fig 7.2 Illustration of bat movement within the boundaries of a defined woodland. Dots represent changes in the position of flying bats every iteration (from Batmodel 1)

7.2.1.5 Moving the observer

In those versions of the model where the observer was not stationary, the observer was moved from a point equidistant from both Y axis boundaries and the lower X axis boundary, to a similar point at the other end of the wood. Movement was at a constant rate in a direction parallel to the Y axis boundary of the wood.

7.2.2 Physical parameters of the model

7.2.2.1 Run time of model

This was based on field work conducted in 1995 and 1996. Where the observer was stationary, the model was run for 300 seconds as this was the length of time spent observing in each microhabitat in Chase Wood, 1996 (see section 2.3.2). Run time for those models where the observer was moving was set equal to the length of the transect divided by the speed of the observer.

7.2.2.2 Iterations of model per second

With a high number of iterations per second, the chances of missing a bat which enters the observation circle briefly are lowered. However, a high number of iterations per second increases the length of computer time the model takes to run. The models were run at two iterations per second as a human observer is unlikely to be able to observe more than two bats per second.

7.2.2.3 Speed of bat flight

Jones and Rayner (1987), examined flight speeds of commuting and foraging *P. pipistrellus*. They found that commuting individuals flew 1.64 times faster than foraging individuals. Mean flight speed during foraging was 4.54ms^{-1}. Mean straight search flight speed for *P. pipistrellus* was found by Kalko (1995) to be 6.3ms^{-1} for the 45kHz phonotype, and 4.2ms^{-1} for the 55kHz phonotype. Most of the bats observed during field work were 45kHz pipistrelles (see section 4.3.1). Bats flying in woodland are unlikely to maintain the speed of straight search flight due to clutter and prey consumption. From a combination of the results of the above two authors, flight speed was set to 4ms^{-1} in the model.

An increase to flight speed in a model may increase the number of bat passes recorded, however the nature of the relationship between bat density and bat activity would be unlikely to differ.

7.2.2.4 Radius of bat flight circles (where applicable)

Models were run using values for the radius of bat flight circles of 10m and 20m.

7.2.2.5 Observation range

The range of the Bat Box III has been estimated at 30m (Tangney and Fairley, 1994). However, a bat 30m from the detector will not be observed unless the detector is pointing in its approximate direction. For the purposes of this model, bats were considered to be detectable when they were within a section of a disc (angle 120°) of radius 30m, centred on the observer. This disc section has the same area as a circle of radius 17.32m, so bats were considered to be in observation range when they were within 17.32m of the observer. This equivalence is acceptable because bats were distributed uniformly and randomly throughout the model wood.

7.2.2.6 Length of transect

This was set to 200m, therefore representative of a typical transect walked, in 1995, in a small woodland (e.g. Fig 2.4 b).

7.2.2.7 Woodland size

For the case where the observer was stationary and bats were moving in circles: if the wood was of infinite size many of the bats would be unobservable (i.e. they could never come into range). Unobservable bats are excluded from the model, where possible, because fluctuations in numbers of unobservable bats cannot affect recorded bat passes in reality. Therefore, the

size of the wood was set so as to include all bats which would come into observation range if the wood was of infinite size, and to exclude as many unobservable bats as possible. The length and width of the woodland were defined as twice the observation range plus twice the radius of bat flight circles, keeping the woodland square for ease of computation.

Because the woodland is square, any bat with its origin in the shaded area in Fig 7.3 is unobservable.

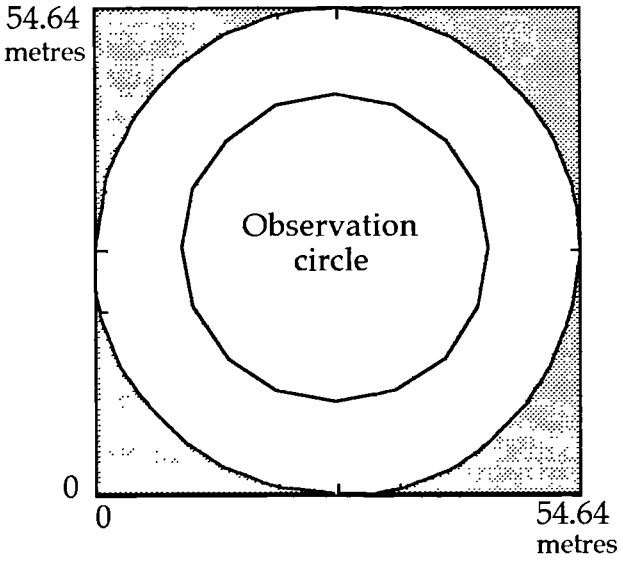


Fig 7.3 Illustration of a model woodland. If the origin of a bat's flight circle is situated in a shaded area the bat is unobservable.

The unshaded area occupies approximately 78.5% of the woodland. Therefore, 78.5% of bats whose flight circles' origins are randomly distributed throughout the woodland are observable.

For ease of comparability between models, for the case where the observer is stationary and the bats are moving randomly the size of the woodland was set so that 78.5% of bats were observed at least once during each run of the model. For this model, woodland size was set to 78m x 78m.

For those versions of the model where the observer was not stationary the X axis boundary of the woodlands were set as before and the length of the transect was added to the Y axis boundary, giving a rectangular woodland.

7.2.2.8 Speed of observer

Walking speed was set to $1ms^{-1}$ ($3.6kmhr^{-1}$). This is a little slower than normal walking speed ($4\text{-}5kmhr^{-1}$), however walking within woodlands at night is invariably slower than over open ground.

7.2.3 Model assumptions

Computer models are limited by the assumptions made. Assumptions were made that:

1 A three dimensional scenario of bats flying at different heights may be projected onto a two dimensional plane
2 Bats are travelling at a constant speed
3 Observer, where applicable, is moving at a constant speed
4 Detection distance is constant
5 Bats move in a similar manner to their movement in the model

The models were coded in Basic by Cormac Parle (see Appendix III).

7.2.4 Running the models

Four versions of the model were run:

1 Stationary observer, bats flying in circles
2 Stationary observer, bats flying randomly
3 Observer moving along transect, bats flying in circles
4 Observer moving along transect, bats flying randomly

The models were run for 50 repetitions with one bat. Bat numbers were incremented by 1 and the models run again 50 times. This was repeated, incrementing by 1 until there were 15 bats present, then by 5 until there were a 100 bats, by 10 until there were 250 bats and by 50 thereafter until the number of bat passes recorded in each run of the model passed realistic limits.

7.2.5 Model checking

Checks were carried out to ensure each model was running correctly and that bat passes were being recorded when the criteria listed above were met (section 7.2.1.3). Figs 7.4 to 7.7 illustrate bat movement, where appropriate, observer movement, and the tally of bat passes with each iteration for Batmodels 1 to 4. In Fig 7.4, two bats enter the observation circle but are not recorded because other bats are closer to the observer at that iteration. This example illustrates that bat passes are only recorded when all criteria are met.

7.2.6 Nonlinear regression

The relationship between mean number of bat passes and bat density was investigated using nonlinear regression as described in Chapter 4 (section 4.2.2.2). Equations investigated as possible fits included:

$$Y = X^{\alpha}$$

$$Y = 1 / (1 + \alpha X)$$

$$Y = 1 - 1 / X^{\alpha}$$

$$Y = \alpha X^{\beta}$$

$$Y = \alpha X + \beta X^2$$

$$Y = \alpha\beta X / (1 + \beta X)$$

where Y is the mean number of observed bat passes and X is the known density of bats. α and β are parameters to be determined by the nonlinear

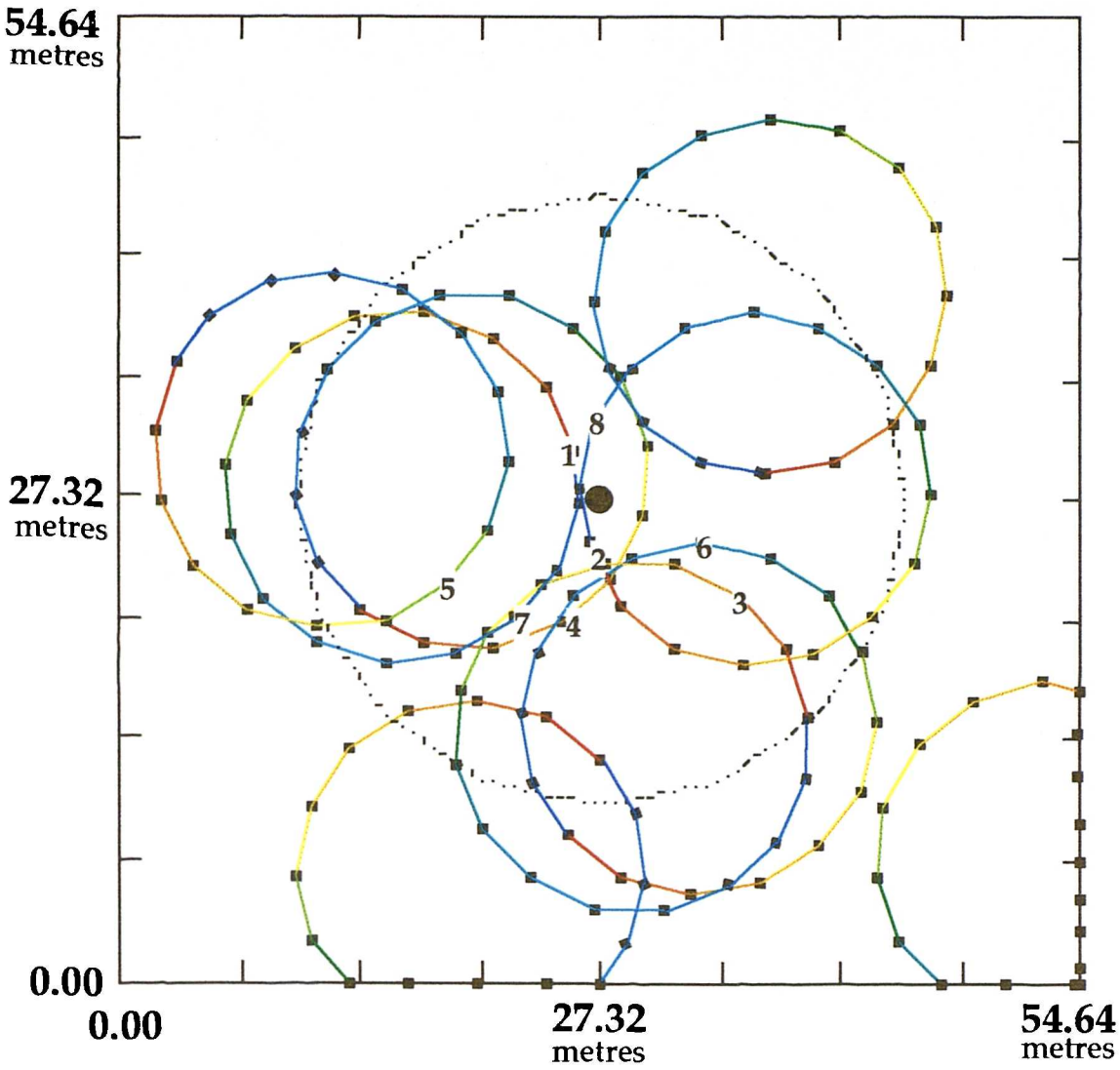


Fig 7.4 Batmodel 1: Illustration of bats' positions and the tally of bat passes. Observer is stationary in centre of wood, observation circle is indicated by dotted black line. Bats' circular flight paths are illustrated in multi-colour. Bats are moving in an anti-clockwise direction. Points on bat flight circles represent their positions on consecutive iterations. The first iteration is illustrated in red and the last in dark blue. Numbers indicate an additional bat pass has been counted. In this example, 8 passes are counted during 17 iterations - equivalent to the length of time taken for each bat to complete its flight circle. Note: In this example two bats enter the observation circle but are not recorded as additional bat passes because, in both cases, other bats are closer to the observer.

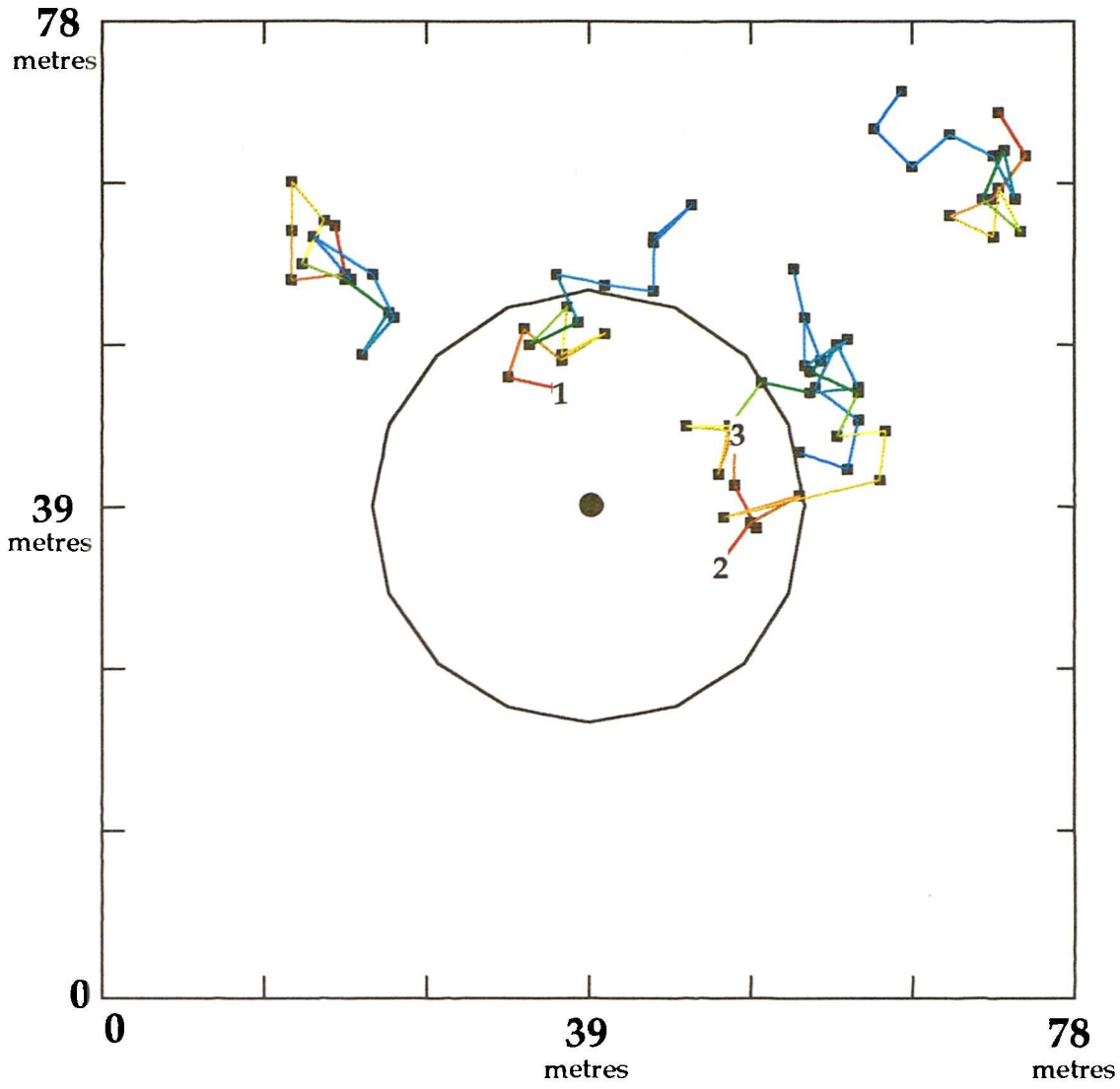


Fig 7.5 Batmodel 2: Illustration of bats' positions and the tally of bat passes. Observer is stationary in centre of wood, observation circle is indicated in black. Bats are moving along random flight paths (illustrated in multi-colour). Points on flight paths represent position of bats on consecutive iterations of the model. The first iteration is illustrated in red and the last in blue. Numbers indicate that an additional bat pass has been counted. In this example, 3 bat passes are counted during the run of the model.

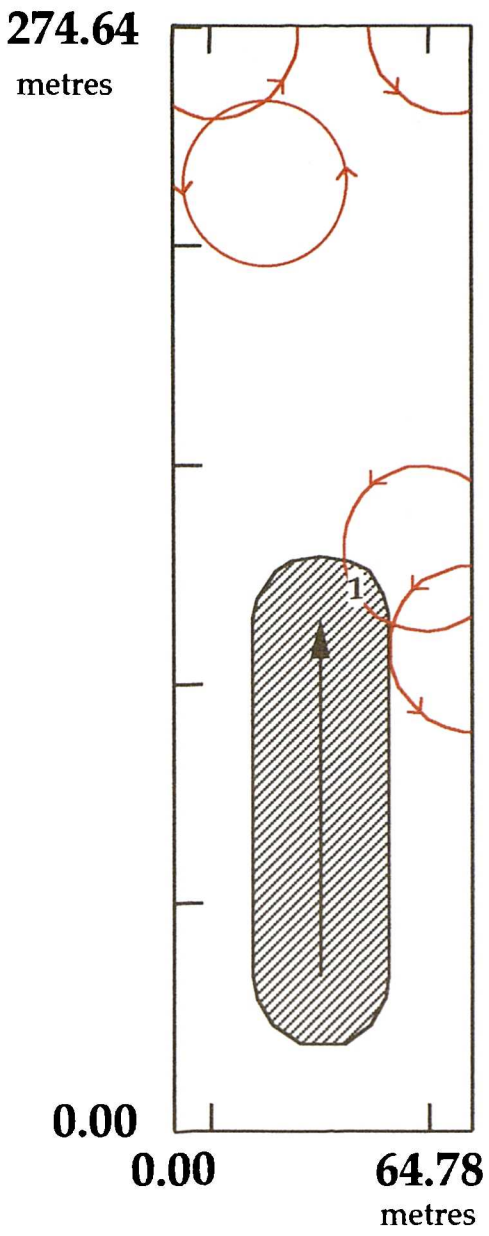


Fig 7.6 Batmodel 3: Illustration of bats' positions and the tally of bat passes. Observer is moving along a transect in the direction of the arrow, path of the observation circle is shown as hatched area. Bats are moving in circles (illustrated in red). 1 bat pass is recorded in this example of the model.

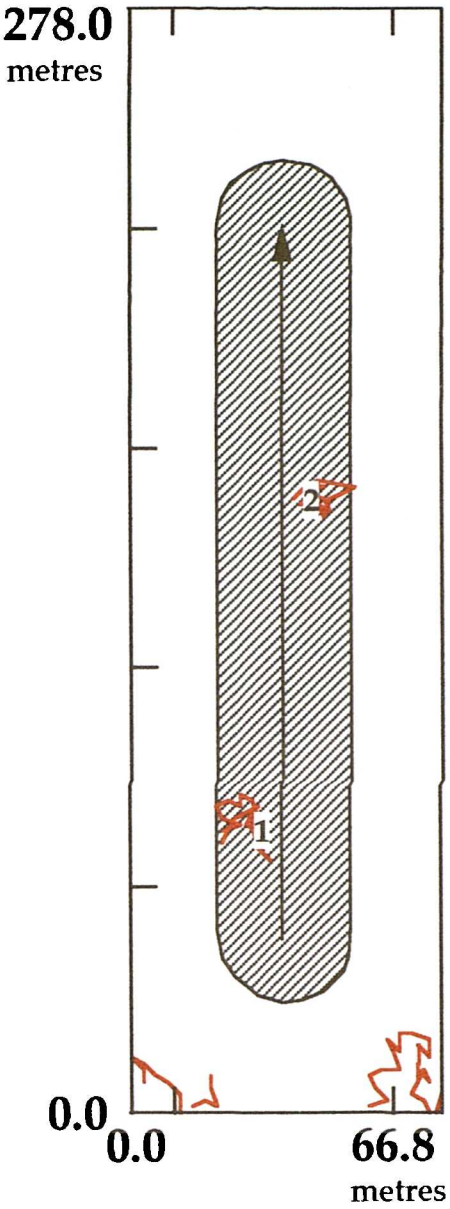


Fig 7.7 Batmodel 4: Illustration of bats' positions and the tally of bat passes. Observer is moving along a transect in the direction of the arrow, path of the observation circle is shown as hatched area. Bats are moving along random flight paths (illustrated in red). In this example, 2 bat passes are recorded

function of SYSTAT 5.2.1. The line was forced through the origin because no bat passes are recorded at a density of zero.

7.3 Results

7.3.1 Stationary observer

Batmodel 1 (radius of bat circles 10m and 20m) & Batmodel 2

Observed bat pass means from Batmodels 1 and 2 are plotted in Fig 7.8.

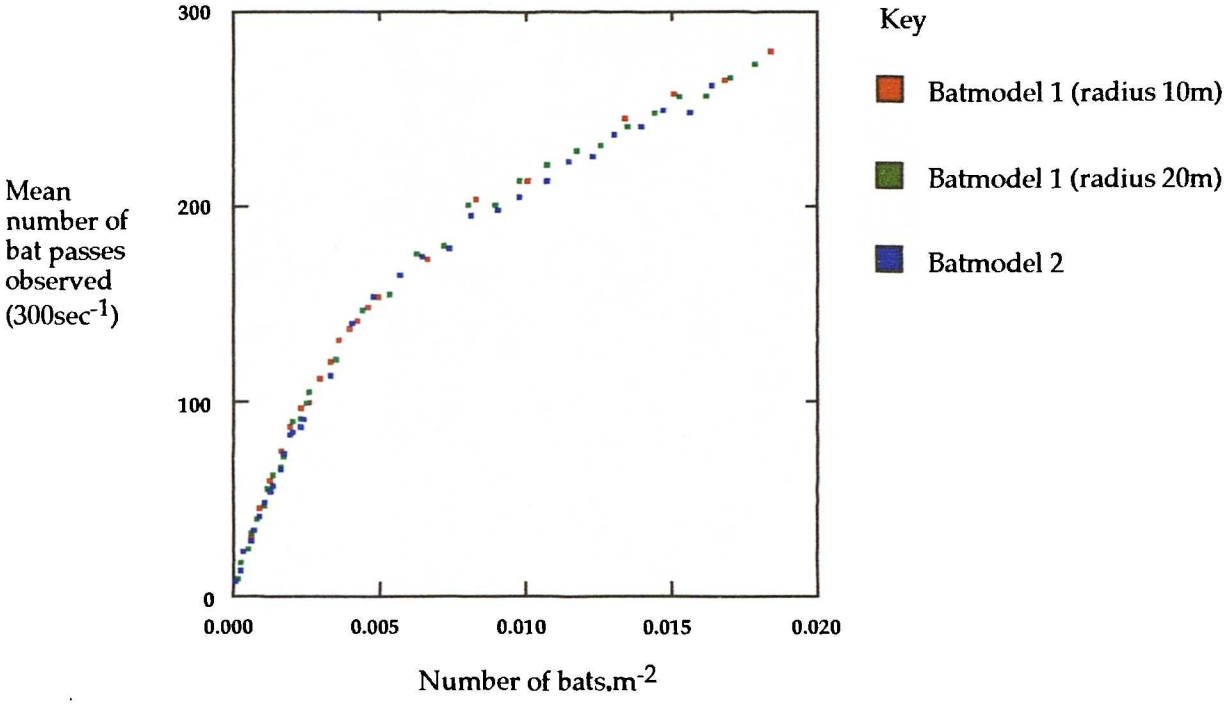


Fig 7.8 Results of Batmodel 1 (flight circle radii of 10m and 20m) and Batmodel 2. Mean number of bat passes observed plotted against density of bats. All three versions show the same relationship between density and passes.

Despite the fact that two different radii were used for bat flight in Batmodel 1, and random flight patterns were used in Batmodel 2, the two models show almost identical results. Bat passes are *almost* linearly related to density at low

values. As bat density increases, the number of observed passes begins to level out.

7.3.2 Moving observer

Observed bat pass means from Batmodels 3 and 4 are plotted in Fig 7.9. Despite the fact that two different flight patterns were used in the two, as in Batmodels 1 and 2, the models show almost identical results. This reinforces the conclusion that flight patterns have little or no effect on mean observations. The nature of the relationship between bat passes observed and density of bats present is the same as for a stationary observer.

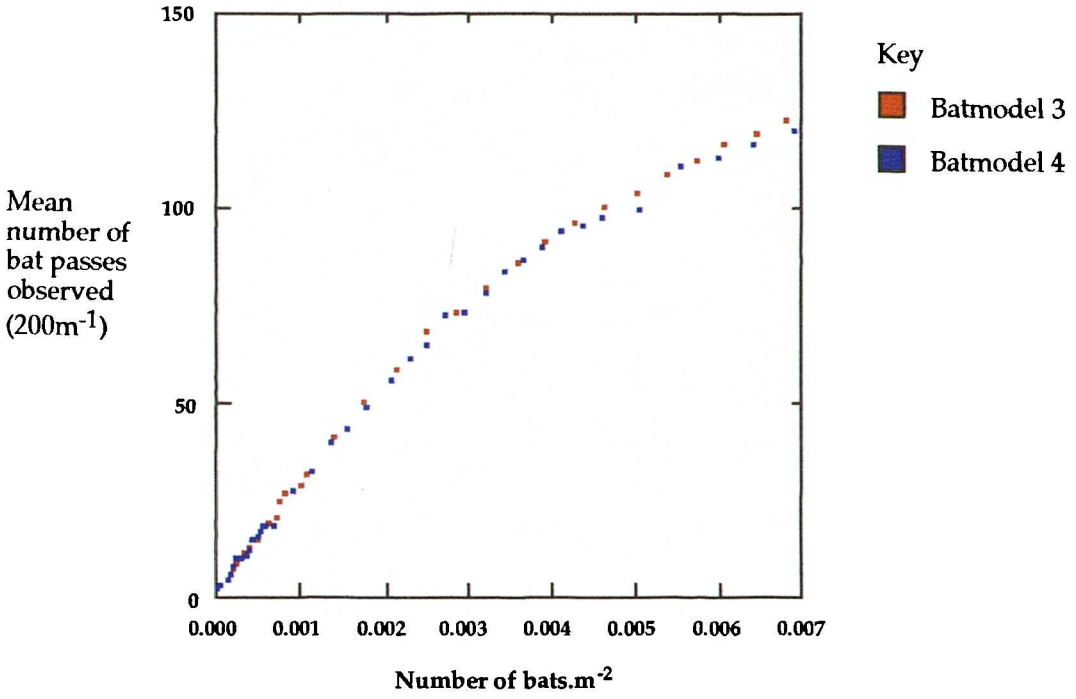


Fig 7.9 Results of Batmodel 3 (flight circle radii of 10m) and Batmodel 4. Mean number of bat passes observed plotted against density of bats. Both versions show the same relationship between density and passes.

7.3.3 Equation of line

The results from each bat model show a similar relationship between bat density and the number of bat passes recorded. The equation best describing this relationship is

$$Y = \alpha\beta X / (1 + \beta X)$$

This accurately fitted results (mean number of passes) of models with stationary and moving observers. An example of this equation fitted to the data of one of the models (Batmodel 2) is shown in Fig 7.10.

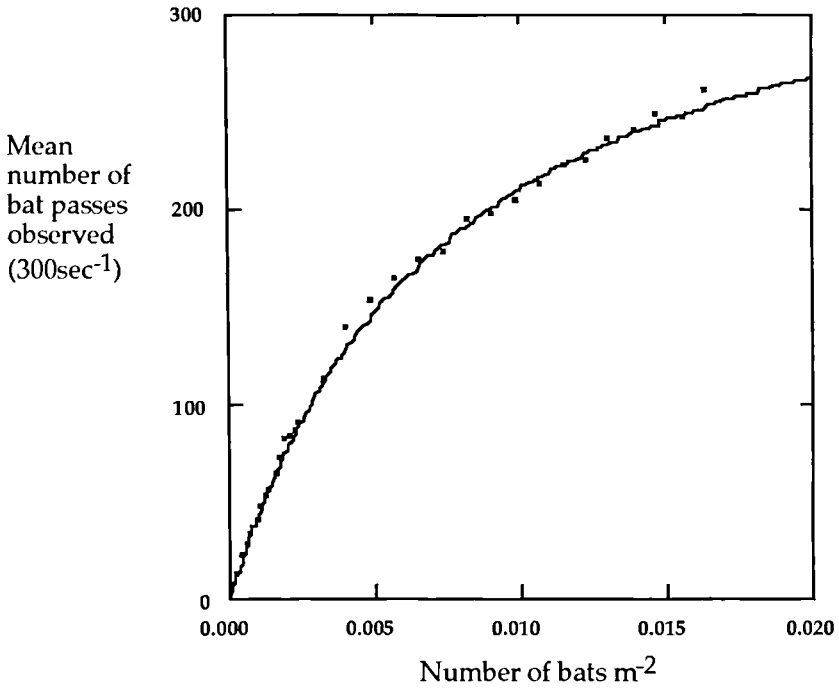


Fig 7.10 Batmodel 2: An example of the fit of equation $Y=\alpha\beta X/(1+\beta X)$ to mean bat pass data.

7.3.4 Variance

While this equation provides an accurate fit to data from models, it would be inappropriate to use it to predict the density of bats present. Fig 7.11 shows means and standard deviations of bat pass data from Batmodel 1

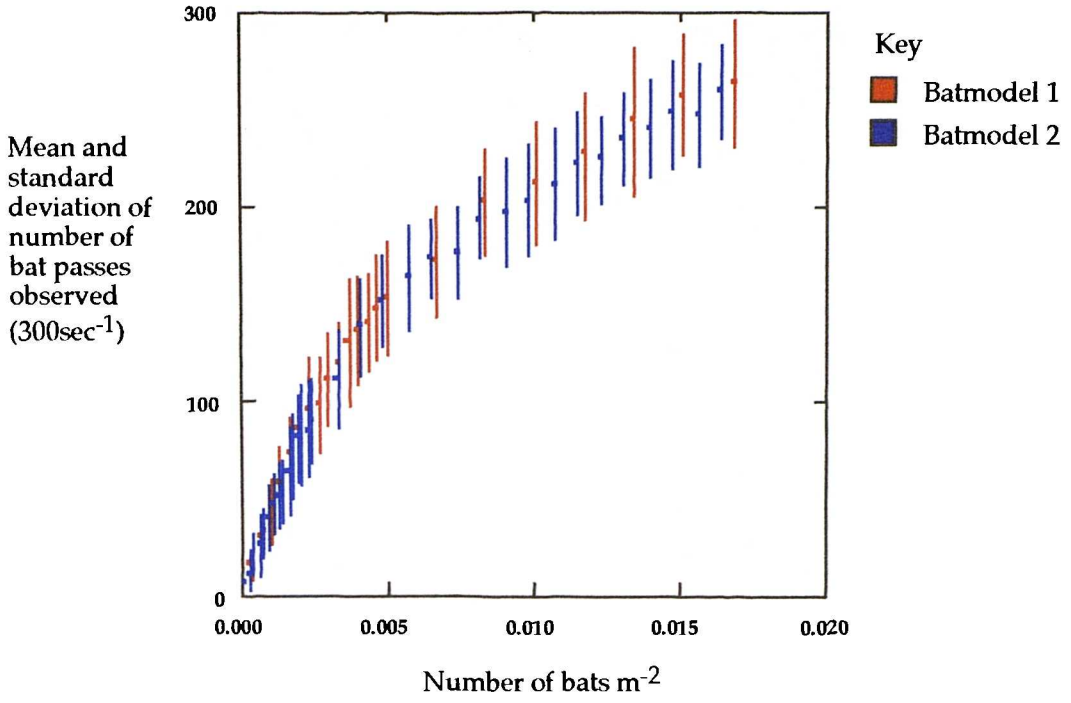


Fig 7.11 Batmodel 1 (radius of bat flight circles=10m) and Batmodel 2: Plot of mean bat passes and standard deviations, against the density of bats present. Standard deviations increase with density.

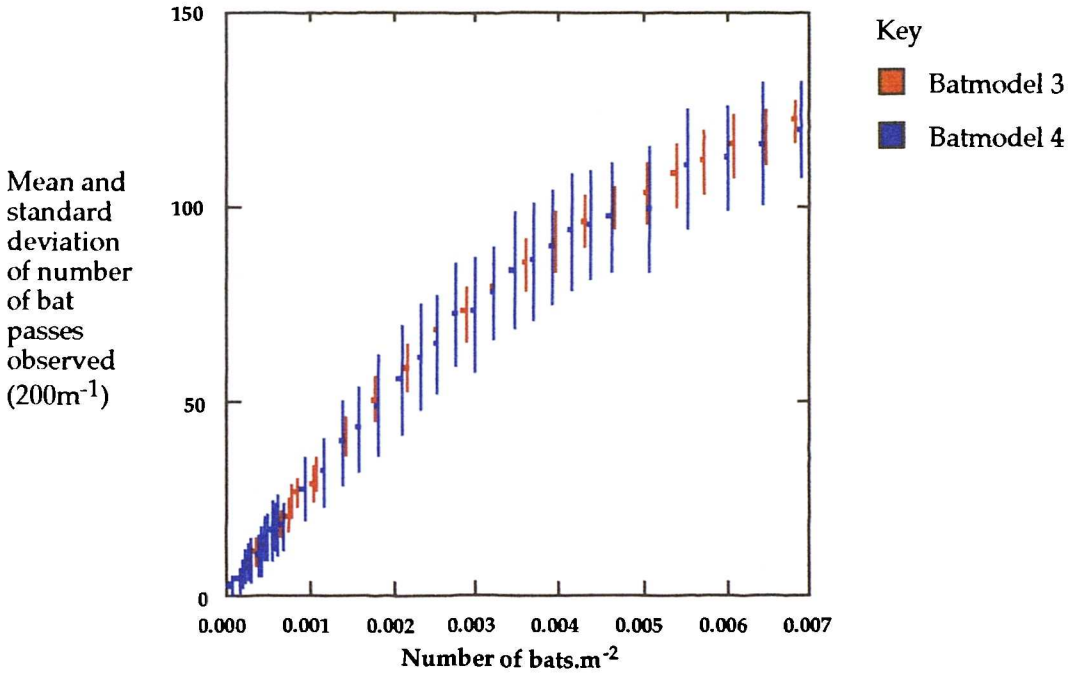


Fig 7.12 Batmodel 3 (radius of bat flight circles=10m) and Batmodel 4: Plot of mean bat passes and standard deviations, against the density of bats present. Standard deviations increase with density.

(radius 10m) and Batmodel 2 and Fig 7.12 shows the equivalent for Batmodels 3 and 4. These graphs show that the standard deviations of bat pass observations increase with bat density. Thus, predictions using the above equation would become more inaccurate with increasing densities.

The standard deviations of Batmodels 3 are lower, in general, than those of Batmodel 4. Therefore, for those models with a moving observer, variation around the mean number of observed bat passes is affected by bat flight pattern, although the mean itself is not. Thus, more information on real flight patterns is necessary in order to allow an accurate estimation of the range of densities associated with a measurement of activity. However, the models as they stand provide some indication of ranges.

Fig 7.13 shows the range covered by standard deviations from Batmodel 1 and 2 estimates.

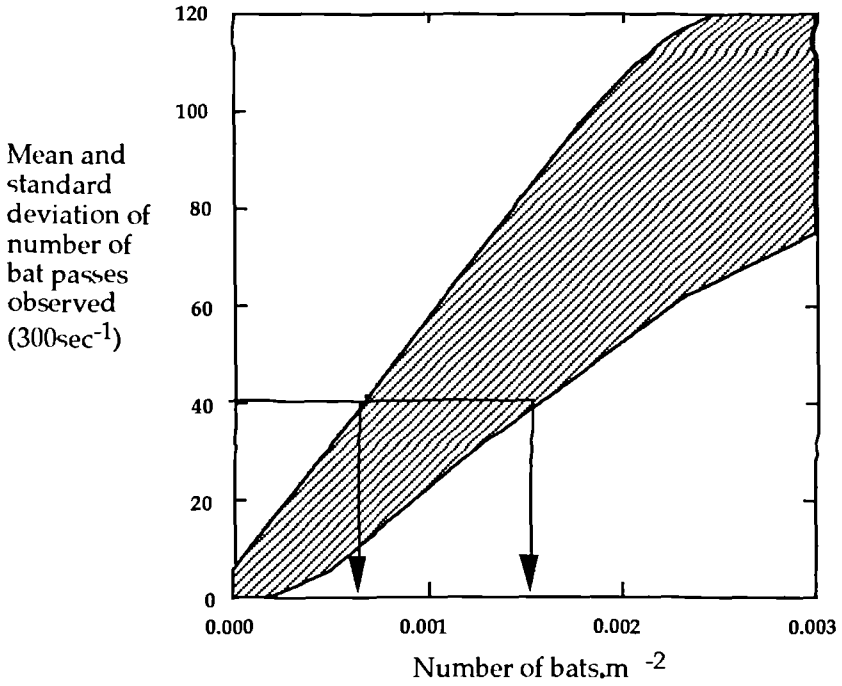


Fig 7.13 Estimating the density of bats present using the number of bats observed per 5 minutes (stationary observer). The shaded area encloses standard deviations of the number of bat passes observed (from Batmodels 1 & 2). 40 bat passes could reflect a density somewhere between 0.0007 and 0.0016bats.m^{-2}

Estimating bat density from 40 bat passes, for example, could pertain to any density from 0.0007 to 0.00164 bats per metre squared. Where a sample is normally distributed, 68.26% of the measurements in a normal population lie within the range of $\mu \pm \sigma$, where μ is the mean and σ is the standard deviation (Zar, 1984). Batmodel samples from low densities (0.0004 and lower) generally deviated significantly from normal. Those above 0.0004 bats. m^{-2} were normally distributed. This underlines the difficulty with making accurate estimations of bat densities, particularly when a low number of bat passes has been observed.

7.3.5 Low bat densities

In the field, the number of bat passes.5 min^{-1} is unlikely to exceed 100. During field work in Chase Wood, 1996, the number of passes did not exceed 30 passes in 5 minutes. The same low values apply to bat passes $metre^{-1}$ in all the woods in 1995. Much higher numbers were reached during Batmodel runs. This is useful because it shows the overall nature of the relationship between bat passes and bat density, however, low bat density values are much more likely to be found in the field. At low values, the relationship between density and passes is reasonably close to linear (Fig 7.14 a&b). However, the same limitation applies to this as to the above equation: that standard deviations increase with density.

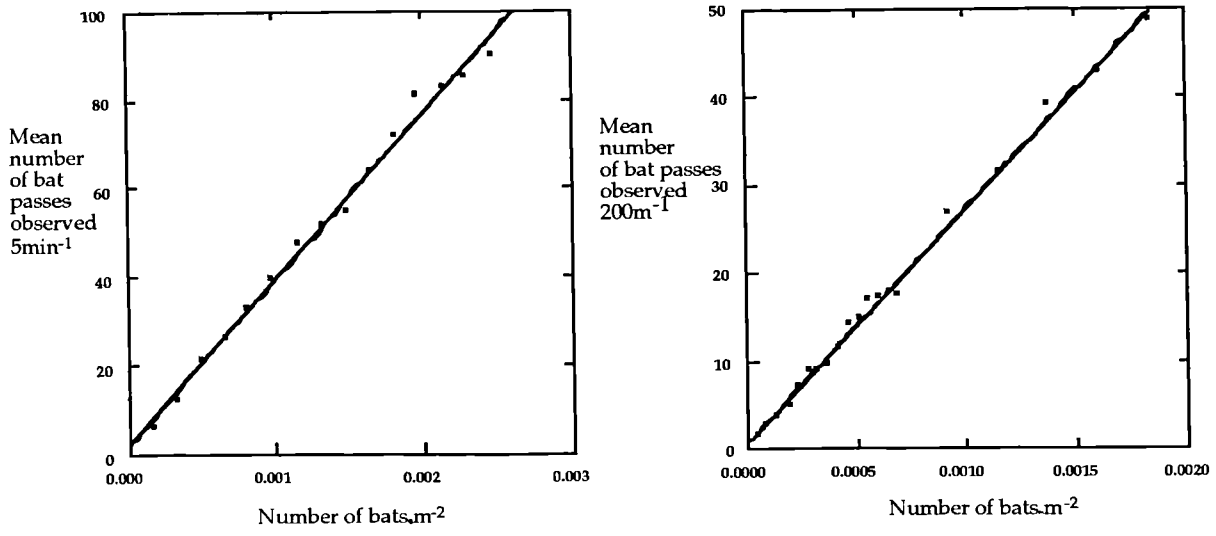


Fig 7.14 a & b Linear smoothing of bat density vs bat passes at activity levels similar to those found in the field. From Batmodels 2 and 4.

7.3.6 Comparing moving and stationary observer models

The data from each model was converted to mean number of bat passes per second. The results for all four models are plotted in Figure 7.15. This shows that the relationship between bat passes and density is unaffected whether the observer is moving (at a constant speed) or stationary.

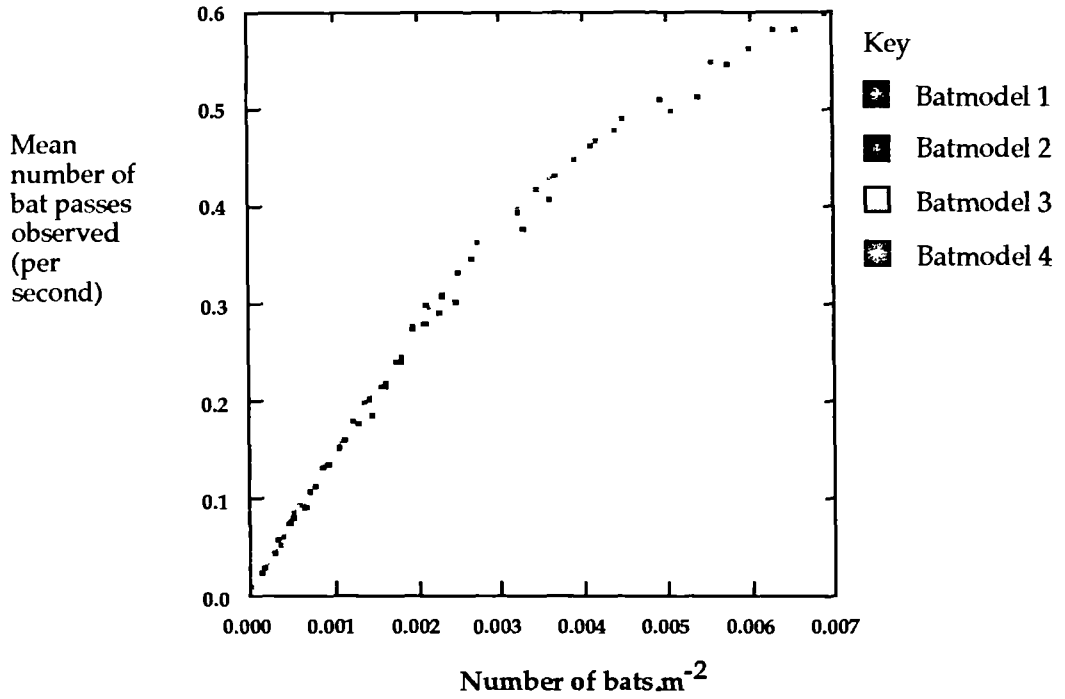


Fig 7.15 Results of the four Batmodels. Mean number of bat passes observed plotted against density of bats. All four show the same relationship between density and passes.

7.4 Discussion

7.4.1 Bat movement

Bats do not fly in circles, nor is it likely that their movements are entirely random. Thus, the definition of bat movement as either circular or random may be a problem with the model. However, the relationship between mean observed bat passes and bat density remained the same despite different bat flight path definitions. This suggests that the relationship between activity and density given by the models is quite robust and is a property of observation method, rather than bat movement. Thus, if the method of observing bats has been modelled in a way which accurately depicts reality, the models are indeed very robust and may be applied to real data.

However, for models with a moving observer, standard deviations of observed bat passes were affected by bat flight pattern. More information on real flight patterns, incorporated into the model, may allow a more accurate estimation of the range of densities associated with a measurement of activity.

7.4.2 The relationship between bat passes and bat density

Overall, a nonlinear relationship between the number of observed bat passes and bat density was found. At low levels of bat activity, similar to those observed in the field, the relationship is close to linear. This is an encouraging result for detector surveying because it indicates that there is a direct relationship between the number of bats observed and the number of bats actually present.

However, it would be inappropriate to predict bat densities using the number of bat passes recorded applied to a straight line equation because of the wide variation typical of bat pass observations. It would be more accurate to estimate the range of densities to which observed bat passes relate. However, at low numbers of bat passes this remains particularly difficult.

The results underline the necessity to obtain repetitive samples when observing bat activity but also indicate that accurate repeated observations will give some indication of the range of densities of bats likely to be present.

Chapter 8

DISCUSSION

8.1 Introduction

Factors influencing spatial and temporal variations in bat activity in deciduous woodlands were examined in this thesis. Vegetation density, insect abundance, weather and the proximity of roosts all combine to affect seasonal bat distribution and nocturnal and seasonal bat activity.

8.2 Methodology

Questionnaires have been used occasionally with reference to wildlife, but rarely on bats. The questionnaire survey used in this study provided useful information on the distribution of roosts in buildings which was found to be a likely factor regulating activity in nearby woodlands. The location lends itself to a survey using questionnaires because there is a high level of interest in wildlife issues in the area, and the landscape is likely to provide suitable bat roosting and foraging habitat. The technique is relatively inexpensive and could be used in other regions where roost data are lacking. Compared with other methods of locating roosts, it requires low levels of manpower.

Roosts were mainly identified as those of *P. pipistrellus* and *P. auritus*. Bat roost densities calculated from questionnaire returns were generally higher than those found by other authors. This may be because no upland/heathland or other habitats unfavourable to bats were included in the survey areas. A higher density of *P. pipistrellus* roosts was located in and around urban areas than in rural areas, and the opposite was true of *P. auritus*. This was similar to findings by Jones *et al.* (1996).

Despite the high number of *P. auritus* roosts located using questionnaires, these bats were rarely detected using the heterodyne detector

during field work. Limits of bat activity estimation have been discussed in detail in Chapter 1 (section 1.2.6.2). As expected, quiet echolocators such as *P. auritus* were rarely observed. Bats with intense echolocation and peak frequencies between 40kHz and 55kHz were most commonly observed. *P. pipistrellus* constituted over 70% of the passes recorded and *Myotis* spp. most of the remainder. Results presented in the thesis mainly refer to pipistrelle activity data. From county records (WBRC), it is likely that *M. mystacinus* (whiskered bat) was the most commonly observed *Myotis* species.

The two *P. pipistrellus* phonotypes were distinguished from July 1995 onwards and the 45kHz type was most common. The 55kHz type may be less prevalent in Warwickshire, but may also prefer riverine habitats (Vaughan, 1996).

Different methods were used to estimate activity in 1995 and 1996 and this complicates comparisons between the two years. However, from the computer simulation, both methods of observing bat passes, from a stationary position (1996) and from a transect (1995), are likely to produce results which correlate with the numbers of bats present. Computer simulations demonstrated a nonlinear correlation between the number of bat passes and the density of bats present. At low levels of bat activity this relationship is close to linear. Therefore, when repeated observations at the same site reveal wide fluctuations in the number of bat passes, this probably reflects changes in the number of bats present.

This is the first time that computer simulations have been used to determine the relationship between bat passes and bat densities, and the results encourage the continued use of bat detectors in habitat survey work.

Insects are unevenly distributed in space (Peng *et al.*, 1992; Williams 1939) and time (Lewis and Taylor, 1964; Davis, 1983) and as a result of these factors, along with the prey avoidance tactics found in many insect orders, it

is difficult to establish precisely the insect types available to a foraging bat.

The three different methods of capturing insects functioned satisfactorily. However, the suction trap is biased toward small aphid sized insects and the light trap captures insects which are attracted to the UV part of the light spectrum, particularly moths. Sweep net samples included many insects which were probably resting or feeding on foliage and may not have been available to foraging *P. pipistrellus*. However, many of the *Myotis* spp. glean some prey and may, therefore, utilise these invertebrates.

Weather data taken from Bablake Weather Station were more often significantly regressed against bat activity and insect availability data, than climate data collected within woodlands during field work nights. From Appendix II.i it can be seen these two datasets were significantly correlated. However, Bablake variables were measured over 24hrs (day and night) and daytime weather conditions may affect insect emergences (and therefore bat activity) more than nightly weather conditions.

8.3 Spatial variations in bat activity

8.3.1 Between woods

Relative bat activity along transects (1995) did not differ significantly between woods. Although this may indicate a similar level of activity throughout each woodland, transects did not cover microhabitats in proportion to their areas within woodlands so such a conclusion could be ill-founded.

Insect densities were also found, from each of the sampling methods, not to differ significantly between woodlands. This is surprising given the differences in size and vegetation diversity between the four woodlands.

Diversity of light trap samples varied a little between woods (Simpson's index). Roughknowles Wood showed greatest light trap catch diversity. The light trap probably had a wider catchment area there compared with the other three woodlands. Diversity of sweep net and suction trap samples did not vary significantly between woodlands.

8.3.2 Between microhabitats

Bat activity was not evenly distributed within woodlands. Preference for, and avoidance of, certain microhabitats was found among both *P. pipistrellus* and *Myotis* spp.

In this study, edges were uniformly avoided by bats throughout the 1995 season. This may have been because 1995 was particularly dry and hot. A positive relationship between humidity and activity at edges, and a negative relationship between humidity and activity within a woodland may be expected if bats were avoiding edges because these areas were not humid enough. However, little evidence was found from multiple regression with climate variables to support this hypothesis, although in 1996, a cooler and wetter year than 1995, the Chase Wood edge was used by *P. pipistrellus* in proportion to its availability.

Insect density was higher at edges than in other woodland microhabitats. Insect abundance was found to decrease with increasing vegetation levels. Therefore, because edges were avoided, microhabitat selection by bats was not based upon a preference for highest relative prey availability.

In contrast to the edge avoidance found in this thesis, previous work on microhabitat use has generally described high bat activity at edges and in open areas within woodlands, and low activity in dense vegetation. From this, a negative linear relationship may have been expected between bat

activity and vegetation levels. In this study, because edges were avoided, activity in woodland microhabitats was best described using a nonlinear equation.

P. pipistrellus activity was plotted against an index of vegetation density of the shrub and canopy layers, or canopy cover abundance (%). A resulting nonlinear equation describing the relationship between vegetation and activity, showed that activity increased linearly to peak at optimum vegetation levels. This peak in activity occurred in natural glades: preferred microhabitats of *P. pipistrellus* in 1995 and 1996. Then, activity decreased exponentially as vegetation became more dense. 1996 *P. pipistrellus* data also fit this nonlinear model. Although *Myotis* spp. also selected natural glades, there were insufficient data on this group of species to apply the model.

Little bat activity was noted in densely vegetated microhabitats. These microhabitats were largely avoided by pipistrelles because their morphology and echolocation are better adapted to more open areas. Dense vegetation was used in proportion to its availability by *Myotis* spp. *M. mystacinus* gleans a large proportion of its prey (Hollyfield, 1993) and, although it is predicted to be a similar flier to the pipistrelle (Norberg and Rayner, 1987), it can hover closely to vegetation (Hollyfield, 1993).

If enough data on activity of *M. mystacinus* and other more manoeuvrable bat species were available to apply the model, it is likely that greatest activity would be located in microhabitats of denser vegetation: optimum vegetation density being dependent on the species' manoeuvrability and echolocation characteristics.

8.4 Temporal variations in bat activity

8.4.1 Nocturnal activity

In two of the study woodlands where a roost had been located nearby (Chase and Tocil), variations in *P. pipistrellus* activity during the night were similar to patterns of activity observed at a pipistrelle roost in Oxfordshire, by Maier (1992). Alterations to activity patterns corresponded to changes in female reproductive condition, as found by Maier (1992) and Swift (1980). Patterns of activity were unimodal, with a peak either around dusk or later in the night, during pregnancy. During lactation activity was bimodal and, post-lactation activity became unimodal again.

These patterns were not followed in Roughknowles Wood. Activity there was particularly low during the time corresponding to lactation, perhaps because there were no proximate roosts. Roost site locations may therefore affect activity levels and should be considered when carrying out surveys of activity in a habitat.

Insect abundance in the suction trap was greatest immediately after dusk. Occasionally, a second pre-dawn peak in insect abundance was apparent. Nocturnal bat activity patterns in different woodlands corresponded to insect availability (from suction trap samples) in late-June, 1995. This time period coincided with lactation. Lactation places high energy demands on females and discourages flight in areas with low insect density, therefore fewer bats may be active at times (or in areas) of low availability. Females also return to the roost during the night to suckle young and this may cause the observed activity trough.

During other months, insect availability and nocturnal activity did not appear to correlate although the possibility remains that suction trap samples did not accurately reflect the prey available to *P. pipistrellus*.

8.4.2 Seasonal activity

In 1995, *P. pipistrellus* activity in each woodland was greatest from late-May to August in each woodland. There were several peaks in activity during that time although a high level was maintained in every woodland, except Roughknowles where activity dropped substantially in late-June.

The suction trap was considered likely to provide the best reflection of the insects available to *P. pipistrellus*. However, seasonal activity of pipistrelles from all four woodlands combined (and from some individual woodlands and microhabitats) was significantly correlated with sweep net numbers. *Myotis* spp. activity from all four woodlands was also significantly correlated with sweep netted invertebrate numbers.

Sweep net samples peaked from mid-June, corresponding to the time of parturition among *P. pipistrellus*. The estimated time of parturition and onset of lactation also coincided with the first peaks in suction trap numbers in all four woodlands, although a second higher peak occurred in early August in three woodlands.

From multiple regression with weather variables, overall *P. pipistrellus* activity (from all four woodlands combined) was most significantly regressed against soil temperature, whilst overall *Myotis* spp. activity was best predicted using a combination of barometric pressure and relative humidity in 1995. In individual woodlands and microhabitats, *P. pipistrellus* activity was usually best described by temperature and/or relative humidity. *Myotis* spp. activity, on the other hand, was rarely significantly predicted using temperature - other variables such as windspeed and barometric pressure were significant regressors.

Bat activity and temperature were positively correlated in 1995. A positive association between temperature and insect abundance has been well documented (e.g. Wellington, 1945). In contrast, relative humidity was usually negatively correlated with bat activity. Peng (1991) found that many

dipterans preferred dry weather for flight, resulting in a negative correlation between humidity and insect availability. Adam *et al.* (1994) found a positive correlation between bat activity and relative humidity and suggested that this was a mechanism used by bats to help prevent water loss. However, in this study relative humidity and water balance did not appear to play an important role determining bat activity.

When multiple partial correlation was carried out with insect numbers included, temperature and relative humidity rarely remained significantly correlated variables. This suggests that relative humidity and temperature directly affected insect abundance and, as a result, indirectly influenced *P. pipistrellus* activity.

Correlations between *Myotis* spp. activity in microhabitats and windspeed remained significant even with the inclusion of insect data in multiple partial correlation analysis. This suggests that windspeed is a physical factor directly affecting *Myotis* spp. activity in those microhabitats. Likewise, the activity of *Myotis* spp. in all four woodlands combined, remained significantly correlated with barometric pressure even when insect data were included in the analysis. *P. pipistrellus* rely mainly on aerial insect fauna, the flight of which are directly affected by temperature. However, *Myotis* spp. glean some of their prey at least and, thus, may not be affected by temperature to the same extent as *P. pipistrellus*.

Barometric pressure may influence bat activity irrespective of insect abundance. Barometric pressure has rarely been investigated as a determinant of bat activity, however, recent research suggests that bats roosting in caves may track barometric pressure and use it to predict insect availability (Paige, 1995). A long term study may reveal more definitively, the importance of barometric pressure as a factor affecting bat activity in woodland.

Rainfall was very low in 1995 and was rarely a significant predictor of bat activity.

In 1995, bat activity in selected (preferred) microhabitat types was not predicted by one particular climate variable (such as minimum temperature (Walsh and Mayle, 1991)). There was no discernible pattern, across all four woodlands, to the variables predicting activity in microhabitat types.

In individual woodlands, certain climate variables were most often significantly correlated with *P. pipistrellus* activity in microhabitats during 1995. These predictor variables may be explained by woodland situation and structure. For example, maximum temperature was the weather variable most often significantly correlated in Long Itchington Wood microhabitats. This woodland has a particularly dense canopy and high temperatures are probably required to facilitate insect emergences there.

In Roughknowles Wood (1995), windspeed and barometric pressure best described bat activity in different microhabitats. The canopy in Roughknowles is very open and, therefore, aerial insects are vulnerable to high windspeeds. Barometric pressure may also be important because insects emerge during the hot and dry weather associated with summer anticyclones.

Nematoceran Diptera were the most abundant insects in suction trap catches. These flies have been found to comprise a high proportion of *P. pipistrellus* diet (Barlow, 1997; Sullivan *et al.*, 1993; Swift *et al.*, 1985). Some significant correlations were found in different woodlands between Cecidomyiidae or Psychodidae abundance and *P. pipistrellus* activity, although these correlations may have been indicative of some other relationship. Evidence for correlations between *P. pipistrellus* activity and the availability of particular insect taxa is difficult to substantiate. This is because invertebrate families were rarely present in trap samples for more than 5 or 6 nights (out of 12 or 13).

Occasionally, particularly high numbers of *P. pipistrellus* passes were noted simultaneously with high availability of a potential prey taxon. For

example, in Roughknowles Wood, the peak in *P. pipistrellus* activity there coincided with a peak in Psychodidae availability. Psychodidae were found by Barlow (1997) to be a major constituent of the diet of the 45kHz *P. pipistrellus* phonotype. Nevertheless, prey availability is probably of greater importance to bats than prey diversity or range.

8.5 Spatial and temporal variations in bat activity

Microhabitat preferences of *P. pipistrellus* were examined for seasonal changes. Natural glades were preferred and edges were avoided throughout 1995. However, clear-cuts were used in proportion to availability until late in the season when they were selected. This is unlikely to reflect a change in wing loading resulting in a change in habitat use, because females gave birth before late-July. *P. pipistrellus* activity was positively correlated with temperature in both of these microhabitats throughout 1995, even when insect data were included in multiple partial correlation. Selection of this microhabitat by bats, which occurred from late-July onwards, may have been due to insect availability at that time but because of the low number of nights involved, further analysis is unfeasible.

Dense vegetation was used in proportion to its availability early in the season but was often avoided from June onwards. This may have been the result of leaf development in the canopy causing more clutter and effectively excluding flying *P. pipistrellus*.

In 1996, the Chase Wood edge was used in proportion to its availability, it had been avoided by *P. pipistrellus* in 1995. Also, in 1996 in Chase Wood temperature was negatively correlated with pipistrelle activity. This compares with positive correlations between activity and temperature

throughout 1995. It appears that bats were less active in Chase Wood on warm nights in 1996.

8.6 Further study

From initial results, it appears that yearly weather changes may affect habitat use by bats. A long term study of activity in small woodlands may underline their importance, particularly to 45kHz *P. pipistrellus*, during dry years.

It may also be feasible to expand the Batmodels to 3-dimensional simulations and, therefore, allow for more rigorous investigation of the relationship between bat passes and bat numbers.

REFERENCES

Abe S., Takatsuki Y., Handa Y. and Nigi H. (1991). Establishment in the wild of the mongoose (*Herpestes* sp.) on Anami-oshima island. *Honyurui kagku*, **31**, 23-26.

Acharya L. (1992). Are ears valuable to moths flying around lights? *Bat Research News*, **33**, 47.

Adam M.D., Lacki M.J. and Shoemaker L.G. (1994). Influence of environmental conditions on flight activity of *Plecotus townsendii virginianus* (Chiroptera: Vespertilionidae). *Brimleyana*, **21**, 77-85.

Ahlén I. (1980-81). Field identification of bats and survey methods based on sounds. *Myotis*, **18-19**, 128-136.

Ahlén I. (1981). *Identification of Scandinavian bats by their sounds*. Swedish Univ. Agric. Sci., Dept. Wildl. Ecol., **Rep. 6**, Uppsala.

Ahlén I. (1990). *Identification of Bats in Flight*. Swedish Society for the Conservation of Nature, Sweden.

Aldridge H.D.J.N. and Rautenbach I.L. (1987). Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology*, **56**, 763-778.

Anderson M.E. and Racey P.A. (1991). Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. *Animal Behaviour*, **42**, 489-493.

Anderson N.H. (1966). Depressant effect of moonlight on activity of aquatic insects. *Nature*, **209**, 319-320.

Anthony E.L.P., Stack M.H. and Kunz T.H. (1981). Night roosting and nocturnal time budget of the little brown bat, *Myotis lucifugus*: Effects of reproductive status, prey density, and environmental conditions. *Oecologia*, **51**, 151-156.

Baagöe H.J. (1987). The Scandinavian bat fauna: Adaptive wing morphology and free flight in the field. In *Recent Advances in the Study of Bats* (Eds

M.B. Fenton, P.A. Racey and J.M.V. Rayner), Cambridge University Press, pp 57-74.

Baines D. and Hudson P.J. (1995). The decline of black grouse in Scotland and northern England. *Bird Study*, **42**, 122-131.

Barclay R.M.R. and Bell G.P. (1988). Marking and observational techniques. In *Ecological and Behavioral Methods for the Study of Bats* (Ed. T.H. Kunz), Smithsonian Institution Press, Washington D.C., pp 59-75.

Barlow K.E. (1997). The diets of two phonic types of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) in Britain. *Journal of Zoology*, in press.

Barratt E.M., Bruford M.W., Burland T.M., Jones G., Racey P.A. and Wayne R.K. (1995). Characterization of mitochondrial DNA variability within the microchiropteran genus *Pipistrellus*: approaches and applications. *Symp. Zool. Soc. Lond.*, **67**, 377-386.

Bassett J.E. (1980). Control of post-prandial water loss in *Myotis lucifugus*. *Comparative Biochemistry and Physiology*, **65A**, 497-500.

Bassett J.E. and Wiebers J.E. (1980). Effect of food consumption on water loss in *Myotis lucifugus*. *Journal of Mammalogy*, **61**, 744-747.

Bauerová Z. and Cerveny J. (1986). Towards an understanding of the trophic ecology of *Myotis nattereri* (Kuhl 1918). *Folia Zoologica*, **35**, 55-61.

Bellamy P.E., Hinsley S.A. and Newton I. (1996). Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology*, **33**, 249-263.

Belwood J.J. and Fenton M.B. (1976). Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology*, **54**, 1674-1687.

Bidlingmayer W.L. (1964). The effect of moonlight on the flight activity of mosquitoes. *Ecology*, **45**, 87-94.

Blake D., Hutson A.M., Racey P.A., Rydell J. and Speakman J.R. (1994). Use of lamplit roads by foraging bats in southern England. *Journal of Zoology, Lond.*, **234**, 453-462.

Bourque L.B. and Fielder E.P. (1995). *How to Conduct Self-Administered and Mail Surveys*. SAGE Publications, Thousand Oaks, 223pp.

Bowden J. (1973). The influence of moonlight on catches of insects in light-traps in Africa. Part I. The moon and moonlight. *Bulletin of Entomological Research*, **63**, 113-128.

Bowden J. and Dean G.J.W. (1977). The distribution of flying insects in and near a tall hedgerow. *Journal of Applied Ecology*, **14**, 343-354.

Bowden J. and Morris M.G. (1975). The influence of moonlight on catches of insects in light-traps in Africa. Part III. The effective radius of a mercury-vapor light-trap and analysis of catches using effective radius. *Bulletin of Entomological Research*, **65**, 303-348.

Bradley G.H. and McNeel T.E. (1935). Mosquito collections in Florida with the New Jersey light trap. *Journal of Economic Entomology*, **28**, 780-786.

Brigham R.M. and Saunders M.B. (1990). The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in Southern Alberta, Canada. *Northwest Science*, **64**, 7-10.

British Geological Survey (1984). *Warwick, Sheet 184: Solid and Drift Edition*. Natural and Environment Research Council.

Burton J. (1968). *The Illustrated Book of Insects*. Oxford University Press.

Carpenter R.E. (1969). Structure and function of the kidney and the water balance of desert bats. *Physiological Zoology*, **42**, 288-302.

Catto C.M.C. (1994). *Bat Detector Manual*. The Bat Conservation Trust, London.

Catto C.M.C., Racey P.A. and Stephenson P.J. (1995). Activity patterns of the serotine bat (*Eptesicus fuscus*) at a roost in southern England. *Journal of Zoology, Lond.*, **235**, 635-644.

Chinery M. (1977). *A Field Guide to the Insects of Britain and Northern Europe.* 2nd Edition, Collins, London 352pp.

Coe R.L., Freeman P. and Mattingly P.F. (1950). *Handbook for the Identification of British Insects, Vol. IX, Part 2: Diptera, Nematocera: families Tipulidae to Chironomidae.* Royal Entomological Society of London, London. 217pp.

Colyer C.N. and Hammond C.O. (1969). *Flies of the British Isles*, 2nd Edition. Lowe and Brydone, London.

Constantine D.G. (1970). Bats in relation to the health, welfare and economy of man. In *Biology of Bats Volume II* (Ed. W.A. Wimsatt). Academic Press, New York, pp 320-420.

Copeland R.S. (1986). The biology of *Aedes thibaulti* in northern Indiana. *Journal of American Mosquito Control Association*, **2**, 1-6.

Corbet G.B. and Harris S. (Eds.) (1991). *The Handbook of British Mammals*, 3rd Edition. Blackwell Scientific Publications, Oxford.

Cranbrook Earl of (1963). Notes on the feeding habits of the long-eared bat. *Suffolk Naturalist Transactions*, **11**, 1-3.

Crome F.H.J. and Richards G.C. (1988). Bats and gaps: microchiropteran community structure in a Queensland rainforest. *Ecology*, **69**, 1960-1969.

Davis B.N.K. (1983). *Insects on Nettles, Naturalists Handbook One.* Cambridge University Press, Great Britain.

Day J.F., Curtis G.A. and Edman J.D. (1990). Rainfall-directed behaviour of *Culex nigripalpus* (Diptera: Culicidae) and its influence on St. Louis encephalitis virus transmission in Indian River County, Florida (USA). *Journal of Medical Entomology*, **27**, 43-50.

De Jong J. (1994). *Distribution Patterns and Habitat use by Bats in relation to Landscape Heterogeneity, and Consequences for Conservation.* Ph.D. Thesis, Swedish University of Agricultural Sciences, Sweden.

De Jong J. and Ahlén I. (1991). Factors affecting the distribution pattern in Uppland, central Sweden. *Holarctic Ecology*, **14**, 92-96.

Dean G.J.W. (1974). Effects of parasites and predators on the cereal aphids *Metopolophium dirhodum* (Walk.) and *Macrosiphum avenae* (F.) (Hem., Aphididae). *Bulletin of Entomological Research*, **63**, 411-422.

Degn H.J. (1983). Field activity of a colony of serotine bats (*Eptesicus serotinus*). *Nyctalus*, **1**, 521-530.

Dell'Uomo G. (1967). Un aspiratoire portatile per cattura di zanzare, azionato a batteria. *Rivista di Parassitologia*, **28**, 221-223.

Dillman D.A., Sinclair M.D. and Clark J.R. (1993). Effects of questionnaire length, respondent-friendly design, and a difficult question on response rates for occupant-addressed census mail surveys. *Public Opinion Quarterly*, **57**, 289-304.

Eastcott H. (1996). The Newhaven rabid bat incident - a public health perspective. *Bat News*, **42**, 2.

Eliot-Higgit S. (1995). A study of aerial insects in mixed deciduous woodland. Biology dissertation (unpub.), B.A.qts, University of Warwick.

Entwistle A.C., Racey P.A. and Speakman J.R. (1996). Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Philosophical Transactions of the Royal Society, Lond. B*, **351**, 921-931.

Entwistle A.C., Racey P.A. and Speakman J.R. (1997). Roost selection by the brown long-eared bat *Plecotus auritus*. *Journal of Applied Ecology*, **34**, 399-408.

Erkert H.G. (1982). Ecological aspects of bat activity rhythms. In *Ecology of Bats* (Ed. T.H. Kunz), Plenum, New York, pp 201-242.

Estrada A., Coates-Estrada R. and Meritt D.Jr. (1993). Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography*, **16**, 309-318.

Evans D. (1992). *A History of Nature Conservation in Britain*. Routledge, London. 274pp.

Faure P.A., Fullard J.H. and Barclay R.M.R. (1990). The response of tympanate moths to the echolocation calls of a substrate gleaning bat, *Myotis evotis*. *Journal of Comparative Physiology, A*, **166**, 843-849.

Fenton M.B. (1970). A technique for monitoring bat activity with results obtained from different environments in Southern Ontario. *Canadian Journal of Zoology*, **48**, 847-851.

Fenton M.B. (1986). Design of bat echolocation calls: implications for foraging ecology and communication. *Mammalia*, **50**, 193-203.

Fenton M.B. (1992). *Bats*. Facts on File, New York.

Fenton M.B. and Bell G.P. (1981). Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy*, **62**, 128-136.

Fenton M.B. and Rautenbach I.L. (1986). A comparison of the roosting and foraging behaviour of three species of insectivorous bats (Rhinolophidae, Vespertilionidae and Molossidae). *Canadian Journal of Zoology*, **64**, 2860-2867.

Fenton M.B., Merriam H.G. and Holroyd G.L. (1983). Bats of Kootenay, Glacier and Mount Revelstoke National Parks Canada: identification by echolocation calls, distribution, and biology. *Canadian Journal of Zoology*, **61**, 2503-2508.

Fenton M.B., Tennant D.C. and Wyszecki J. (1987). Using echolocation calls to measure the distribution of bats: the case of *Euderma maculatum*. *Journal of Mammalogy*, **68**, 142-144.

Findley J.S. (1993). *Bats: a community perspective*. Cambridge University Press, Great Britain. 167pp.

Fletcher R. (1972). FORTRAN subroutines for minimization by quasi-Newton methods. *AERE* R. 7125.

Fowler F.J. (1984). *Survey Research Methods*. SAGE Publications, London.

Fraser F.C. (1959). *Handbook for the Identification of British Insects Vol. 1 Parts 12&13: Mecoptera, Megaloptera and Neuroptera.* Royal Entomological Society of London. 40pp.

Freund J.E. and Simon G.A. (1992). *Modern Elementary Statistics,* 8th Edition. Prentice-Hall International, Inc., New Jersey. 578pp.

Fullard J.H. (1989). Echolocation survey of the distribution of the Hawaiian hoary bat (*Lasiurus cinereus semotus*) on the island of Kaua'i. *Journal of Mammalogy,* **70**, 424-426.

Fullard J.H., Koehler C., Surlykke A. and McKenzie N.L. (1991). Echolocation ecology and flight morphology of insectivorous bats (Chiroptera) in south-western Australia. *Australian Journal of Zoology,* **39**, 427-438.

Fullard J.H., Simmons J.A. and Saillant P.A. (1994). Jamming bat echolocation: the dogbane tiger moth (*Cycnia tenera*) times its clicks to the terminal attack calls of the big brown bat (*Eptesicus fuscus*). *Journal of Experimental Biology,* **194**, 285-298.

Furlonger C.L., Dewar H.J. and Fenton M.B. (1987). Habitat use by foraging insectivorous bats. *Canadian Journal of Zoology,* **65**, 284-288.

Gaisler J., Vlasín M. and Bauerová Z. (1989). The bats of the S-Moravian lowlands over thirty years: small *Myotis*. **38**, 213-225.

Gressitt J.L. and Gressitt M.K. (1962). An improved Malaise trap. *Pacific Insects*, **4**, 87-89.

Griffin D.R. (1969). The physiology and geophysics of bird navigation. *Quarterly Review of Biology,* **44**, 255-276.

Hayes W.L. and Winkler R.L. (1970). *Statistics; Probability, Inference and Decision.* Vol. 1. Holt, Rinehart and Winston, New York. 650pp.

Hickey M.B.C. and Fenton M.B. (1990). Foraging by red bats (*Lasiurus borealis*): do intraspecific chases mean territoriality? *Canadian Journal of Zoology,* **68**, 2477-2482.

Hollyfield A.M. (1993). *Diet in Relation to Prey Availability and the Directionality of Echolocating calls in three Species of British Bats*. Ph.D. Thesis, University of Bristol.

Horsfall W.R. (1943). Some responses of the malaria mosquito to light. *Annals of the Entomological Society of America*, **36**, 41-45.

Husbands R.C. and Holten J.R. (1967). An improved mechanical method of aspirating insects. *Californian Vector Views*, **14**, 78-80.

Johnson C.G. (1950). The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small airborne insects. *Annals of Applied Biology*, **37**, 268-285.

Johnson C.G. and Taylor L.R. (1955). The development of large suction traps for airborne insects. *Annals of Applied Biology*, **43**, 51-62.

Jones G. (1993). Some techniques for the detection, recording and analysis of echolocation calls from wild bats. *Proceedings of the First European Bat Detector Workshop*, (Ed. K. Kapteyn), Netherlands Bat Research Foundation, Amsterdam. pp 25-33.

Jones G. and Rayner J.M.V. (1987). Optimal flight speed in pipistrelle bats (*Pipistrellus pipistrellus*). In *European Bat Research* (Eds V. Hának, I. Horácek and J. Gaisler), Charles University Press, Praha. pp 247-253.

Jones G. and Rydell J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions Royal Society, Lond. B*, **346**, 445-455.

Jones G. and Van Parijs S.M. (1993). Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proceedings of the Royal Society, London*, **251B**, 119-125.

Jones K.E. Altringham J.D. and Deaton R. (1996). Distribution and population densities of seven species of bat in northern England. *Journal of Zoology, Lond.*, **240**, 788-798.

Jones-Walters L.M. (1989). Keys to the families of British spiders. *Field Studies*, **9**, 365-443.

Jorgensen J.M. (1984). Fine structure of the paratympanic organ in the avian middle ear and tympanum. *Anatomical Record*, **190**, 177-200.

Juillet J.A. (1963). A comparison of four types of traps used for capturing insects. *Canadian Journal of Zoology*, **41**, 219-223.

Kalcounis M.C. and Brigham R.M. (1995). Intraspecific variation in wing loading affects habitat use by little brown bats (*Myotis lucifugus*). *Canadian Journal of Zoology*, **73**, 89-95.

Kalko E.K.V. (1995). Insect pursuit, prey capture and echolocation in pipistrelle bats (Microchiroptera). *Animal Behaviour*, **50**, 861-880.

Karg J. (1980). A method of motor-net for estimation of aeroentomofauna. *Polish Ecological Studies*, **6**, 345-354.

Kay B.H. (1983). Collection of resting adult mosquitoes at Kowanyama, northern Queensland and Charleville, south-western Queensland. *Journal of Australian Entomological Society*, **22**, 19-24.

Kennedy C.E.J. and Southwood T.R.E. (1984). The number of species associated with British trees: A re-analysis. *Journal of Animal Ecology*, **53**, 455-478.

Kindvall O. (1995). The impact of extreme weather on habitat preference and survival in a metapopulation of the bush cricket *Metrioptera bicolor* in Sweden. *Biological Conservation*, **73**, 51-58.

Kirby, P. (1992). *Habitat Management for Invertebrates. A Practical Handbook*. RSPB, Bedfordshire.

Kronwitter F. (1988). Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio tracking. *Myotis*, **26**, 23-85.

Krull D., Schumm A., Metzner W. and Neuweiler G. (1991). Foraging areas and foraging behaviour in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). *Behavioural Ecology and Sociobiology*, **28**, 247-254.

Krusic R.A., Yamasaki M., Neefus C.D. and Pekins P.J. (1996). Bat habitat use in White Mountain National Forest. *Journal of Wildlife Management*, **60**, 625-631.

Kunz T.H. (1973). Resource utilization: temporal and spatial components of bat activity in central Iowa. *Journal of Mammalogy*, **54**, 14-32.

Kunz T.H. (1974). Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology*, **55**, 693-711.

Kunz T.H. (1988). Methods of assessing the availability of prey to insectivorous bats. *Ecological and Behavioural Methods for the Study of Bats* (Ed. T.H. Kunz), Smithsonian Institution Press, Washington D.C. pp 191-210.

Kurta A. (1991). Torpor patterns in food-deprived *Myotis lucifugus* (Chiroptera: Vespertilionidae) under simulated roost conditions. *Canadian Journal of Zoology*, **69**, 255-257.

Kurta A., Bell G.P., Nagy K.A. and Kunz T.H. (1989). Water balance of free-ranging little brown bats (*Myotis lucifugus*) during pregnancy and lactation. *Canadian Journal of Zoology*, **67**, 2468-2472.

Kurta A., Kunz T.H. and Nagy K.A. (1990). Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. *Journal of Mammalogy*, **71**, 59-65.

Kutt A.S. (1995). Activity and stratification of microchiropteran bat communities in thinned, unthinned and old lowland regrowth forest, east Gippland. *The Victorian Naturalist*, **112**, 86-92.

Lacki M.J. (1984). Temperature and humidity induced shifts in the flight activity of little brown bats. *Ohio Journal of Science*, **84**, 264-266.

Lawton J.H. (1976). The structure of the arthropod community on bracken. *Botanical Journal of the Linnaen Society*, **73**, 187-216.

Lewis F.P., Fullard J.H. and Morrill S.B. (1993). Auditory influences on the flight behaviour of moths in a Nearctic site. II flight times, heights and erraticism. *Canadian Journal of Zoology*, **71**, 1562-1568.

Lewis T. (1967). The horizontal and vertical distribution of flying insects near artificial windbreaks. *Annals of Applied Biology*, **60**, 23-31.

Lewis T. (1970). Patterns of distribution of insects near a windbreak of tall trees. *Annals of Applied Biology*, **65**, 213-220.

Lewis T. and Dibley G.C. (1970). Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. *Annals of Applied Biology*. **66**, 477-484.

Lewis T. and Taylor L.R. (1964). Diurnal periodicity of flight by insects. *Transactions of the Royal Entomological Society of London*, **116**, 393-476.

Limpens H.J.G.A. (1993). Bat detectors in a detailed survey: a method. In *Proceedings of the First European Bat Detector Workshop* (Ed. K. Kapteyn). Netherlands Bat Research Foundation, Amsterdam. pp 79-90.

Limpens H.J.G.A., Helmer W., Van Winden A. and Mostert K. (1989). Bats (Chiroptera) and linear landscape elements. A review of our present knowledge of the importance of linear landscape elements to bats. *Lutra*, **32**, 1-20.

Limpens, H.J.G.A.. and Kapteyn, K. (1991). Bats, their behaviour and linear landscape elements. *Myotis*, **29**, 63-71.

Magurran A.E. (1988). Ecological Diversity and its Measurement. Croom Helm Ltd., London. 179pp.

Maier C. (1992). Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *Journal of Zoology, Lond.*, **228**, 69-80.

Malaise R. (1937). A new insect-trap. *Entomologisk Tidskrift*, **58**, 148-160.

May R.M. (1975). Patterns of species abundance and diversity. In *Ecology and Evolution of Communities* (Eds M.L. Cody and J.M. Diamond). Harvard University Press, Cambridge, MA, pp 81-120.

Mayle B.A. (1990a). A biological basis for bat conservation in British woodlands - a review. *Mammal Review*, **20**, 159-195.

Mayle B.A. (1990b). Habitat management for woodland bats. *Forestry Commission Research Information Note 165*. Forestry Commission Research Division.

McAney C.M., Shiel C.B., Sullivan C.M. and Fairley J.S. (1991). The analysis of bat droppings. *An Occasional Publication of the Mammal Society*, No. 14.

McAney C.M. and Fairley J.S. (1989). Analysis of the diet of the lesser horseshoe bat *Rhinolophus hipposideros* in the west of Ireland. *Journal of Zoology, Lond.*, **217**, 491-498.

McClure E.H. (1938). Insect aerial populations. *Annals of the Entomological Society of America*, **31**, 504-513.

Miller L.A. and Surlykke A. (1995). How insects detect and avoid bats: the tactics of prey and predator. *10th International Bat Research Conference*, Boston, U.S.

Morrison D.W. (1978). Lunar phobia in the neotropical fruit bat, *Artiblus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour*, **26**, 852-855.

Navo K.W.J., Gore J.A. and Skiba G.T. (1992). Observations of the spotted bat, *Euderma maculatum*, in northwestern Colorado. *Journal of Mammalogy*, **73**, 547-551.

Neal, E. (1958). *Woodland Ecology*, 2nd Edition. Heinemann, Britain.

Negraeff D.E. and Brigham R.M. (1995). The influence of moonlight on the activity of little brown bats (*Myotis lucifugus*). *Zeifschrift fur saugetierkunde - International Journal of Mammalian Biology*, **60**, 330-336.

Neu C.W., Randall Byers C. and Peek J.M. (1978). A technique for analysis of utilization-availability data. *Journal of Wildlife Management*, **38**, 541-545.

Neuweiler G. (1984). Foraging, echolocation and audition in bats. *Naturwissenschaften*. **71**, 446-455.

Neuweiler G. (1989). Foraging ecology and audition in echolocating bats. *Trends in Ecology and Evolution*. **4**, 160-166.

Neuweiler G. (1990). Auditory adaptations for prey capture in echolocating bats. *Physiological Review*, **70**, 615-638.

Norberg U.M. and Rayner J.M.V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London (Biology)*, **316**, 355-427.

O'Farrell M.J. and Bradley W.G. (1970). Activity patterns of bats over a desert spring. *Journal of Mammalogy*, **51**, 133-135.

O'Farrell M.J., Bradley W.G. and Jones G.W. (1967). Fall and winter bat activity at a desert spring in southern Nevada. *South-western Naturalist*, **12**, 163-171.

O'Neill M.G. and Taylor R.J. (1989). Feeding ecology of Tasmanian bat assemblages. *Australian Journal of Ecology*, **14**, 19-31.

Paige K.N. (1995). Bats and barometric pressure: conserving limited energy and tracking insects from the roost. *Functional Ecology*, **9**, 463-467.

Parman D.C. (1920). Observations of the effect of storm phenomena on insect activity. *Journal Economic Entomology*, **13**, 339-343.

Pendleton G.W. (1992). Nonresponse patterns in the federal waterfowl hunter questionnaire survey. *Journal of Wildlife Management*, **56**, 344-348.

Peng R.K. (1991). *The Influence of Microclimate on the Spatial Distribution of Flying I nsects*. Ph.D. Thesis, University of Leeds.

Peng R.K., Sutton S.L. and Fletcher C.R. (1992). Spatial and temporal distribution patterns of flying Diptera. *Journal of Zoology, Lond.*, **228**, 329-340.

Peterken G.F. (1981). *Woodland Conservation and Management*. Chapman and Hall, London.

Peterken G.F. (1991). Ecological issues in the management of woodland nature reserves. *The Scientific Management of Temperate Communities for*

Conservation (Eds I.F. Spellerberg, F.B. Goldsmith and G. Morris), Blackwells, Oxford, pp. 245-272.

Pettersson L. (1993). Ultrasound detectors: different techniques, purposes and methods. *Proceedings of the First European Bat Detector Workshop* (Ed. K. Kapteyn), Netherlands Bat Research Foundation, Amsterdam, pp. 11-13.

Pielou E.C. (1975). *Ecological Diversity.* John Wiley and Sons Inc., New York.

Poole R.W. (1974). *An Introduction to Quantitative Ecology.* McGraw-Hill Kogakusha Ltd., Tokyo.

Poulton E.B. (1929). British insectivorous bats and their prey. *Proceedings of the Zoological Society London*, **1**, 277-303.

Pratt H.D. (1948). Influence of the moon on light trap collections of *Anopheles albimanus* in Puerto Rico. *Jour. Natl. Malaria Soc.* **7**, 212-220.

Provost M.W. (1959). The influence of moonlight on light trap catches of mosquitoes. *Annals of the Entomological Society of America*, **52**, 261-271.

Racey P.A. (1973). Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility, Supplement*, **19**, 175-189.

Racey P.A. (1982). Ecology of bat reproduction. In *Ecology of Bats* (Ed. T.H. Kunz). Plenum Press, New York. pp 57-104.

Racey P.A. and Stebbings R.E. (1972). Bats in Britain - a status report. *Oryx*, **6**, 319-327.

Racey P.A. and Swift S.M. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *Journal of Animal Ecology*, **54**, 205-215.

Racey P.A., Speakman J.R. and Swift S.M. (1987). Reproductive adaptations of heterothermic bats at the northern borders of their distribution. *South African Journal of Science*, **83**, 635-638.

Rachwald A. (1992). Habitat preference and activity of the noctule bat *Nyctalus noctula* in the Bialowieza primeval forest. *Acta Theriologica*, **37**, 413-422.

Ratkowsky D.A. (1990). *Handbook of Nonlinear Regression Models*. Marcel Dekker, New York, 241pp.

Rautenbach I.L., Fenton M.B. and Whiting M.J. (1996). Bats in riverine forests and woodlands - a latitudinal transect in southern Africa. *Canadian Journal of Zoology*, **74**, 312-322.

Rautenbach I.L., Kemp A.C. and Scholtz C.H. (1988). Fluctuations in availability of arthropods correlated with microchiropteran and avian predator activities. *KOEDOE*, **31**, 77-90.

Reling D. and Taylor R.A.J. (1984). A collapsible tow net for sampling arthropods by airplane. *Journal of Economic Entomology*, **77**, 1615-1617.

Roberts M.J. (1985a). *The Spiders of Great Britain and Ireland.* Part 1 - text. Harley Books, England.

Roberts M.J. (1985b). *The Spiders of Great Britain and Ireland.* Part 2 - colour plates. Harley Books, England.

Rydell J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, **6**, 744-750.

Rydell J. and Racey P.A. (1995). Street lamps and the feeding ecology of insectivorous bats. In *Ecology, Evolution and Behaviour of Bats* (Eds P.A. Racey and S.M. Swift). *Symposium of the Zoological Society London*, **67**, 291-307.

Rydell J., Bushby A., Cosgrove C. and Racey P.A. (1994). Habitat use by bats along rivers in North East Scotland. *Folia Zoologica*, **43**, 417-424.

Sankey J.H.P. and Savory T.H. (1974). *British Harvestmen*. Published for the Linnean Society of London, Academic Press, London and New York.

Sargent G. (1995). *The Bats in Churches Project*. The Bat Conservation Trust, London, 48pp.

Service M.W. (1971). The daytime distribution of insects resting in vegetation. *Journal of Medical Entomology*, **8**, 271-278.

Service M.W. (1973a). Flight activities of mosquitoes with emphasis on host seeking behaviour. *Biting Fly Control and Environmental Quality* (Ed. A. Hutson), Proceedings of the Symposium of University of Alberta, Canada. pp 125-132.

Service M.W. (1973b). Spatial and temporal distribution of aerial populations of woodland tipulids (Diptera). *Journal Animal Ecology*, **42**, 295-303.

Service M.W. (1993). *Mosquito Ecology: Field Sampling Methods*. 2nd Edition, Elsevier Science Publishers Ltd., U.K.

Shiel C.B., McAney C.M. and Fairley J.S. (1991). Analysis of the diet of Natterer's bat, *Myotis nattereri*, and the common long-eared bat, *Plecotus auritus* in the west of Ireland. *Journal of Zoology, Lond*, **223**, 299-305.

Simmons K.R., Edman J.D. and Bennett S.R. (1989). Collection of blood-engorged black flies (Diptera: Simuliidae) and identification of their source of blood. *Journal of American Mosquito Control Association*, **5**, 541-546.

Simpson E.H. (1949). Measurement of diversity. *Nature*, **163**, 688.

Smith R.L. (1980). *Ecology and Field Biology*. 3rd Edition. Harper and Row, New York.

South R. (1971a). *The Moths of the British Isles, Series I*. Frederick Warne and Co. Ltd., London and New York.

South R. (1971b). *The Moths of the British Isles, Series II*. Frederick Warne and Co. Ltd., London and New York.

Southwood T.R.E. (1978). *Ecological Methods*. Chapman and Hall, London, 524pp.

Speakman J.R. (1991). The impact of predation by birds on bat populations in the British Isles. *Mammal Review*, **21**, 123-142.

Speakman J.R., Racey P.A., Catto C.M.C., Webb P.I., Swift S.M. and Burnett A.M. (1991). Minimum summer populations and densities of bats in N.E. Scotland, near the northern borders of their distributions. *Journal of Zoology, Lond.*, **225**, 327-345.

Spellerberg I.F. (1992). *Evaluation and Assessment for Conservation*. Chapman and Hall, London.

Stebbings R.E. (1988). *The Conservation of European Bats*. Christopher Helm, London.

Stebbings R.E. (1993). *Which Bat Is It?* The Mammal Society, London.

Steelman C.D., Richardson C.G., Schaefer R.E. and Wilson B.H. (1968). A collapsible truck-boat for collecting blood-fed mosquitoes and tabanids. *Mosquito News*, **28**, 64-67.

Sudia W.D. and Chamberlain R.W. (1967). *Collection and Processing of Medically Important Arthropods for Virus Isolation*. US Dept. Health Education, National Disease Center, Georgia, 29pp.

Sullivan C.M., Shiel C.B., McAney C.M. and Fairley J.S. (1993). Analysis of the diets of Leisler's (*Nyctalus leisleri*), Daubenton's (*Myotis daubentoni*) and pipistrelle (*Pipistrellus pipistrellus*) bats in Ireland. *Journal of Zoology, Lond.*, **231**, 656-663.

Swift S.M. (1980). Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology, Lond.*, **190**, 285-295.

Swift S.M. and Racey P.A. (1983). Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *Journal of Zoology, Lond.*, **200**, 249-259.

Swift S.M., Racey P.A. and Avery M.I. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *Journal of Animal Ecology*, **54**, 217-225.

Taake K.H. (1984). Strukturelle Unterschiede zwischen den Sommerhabitaten von kleiner und großer Bartfledermaus (*Myotis mystacinus* und *M. brandtii*) in Westfalen. *Nyctalus*, **2**, 16-32.

Tangney D.E. and Fairley J.S. (1994). Habitat preferences of bats in Connemara National Park and its environs. *Irish Naturalist's Journal*, **24**, 458-460.

Tasker A. (1991). The Nature of Warwickshire. Barracuda Books, Buckingham.

Taylor J.A. and Yates R.A. (1967). *British Weather in Maps*. 2nd Edition. Macmillan, London.

Taylor L.R. (1951). An improved suction trap for insects. *Annals of Applied Biology*, **38**, 582-591.

Taylor L.R. (1962). The absolute efficiency of insect suction traps. *Annals of Applied Biology*, **50**, 405-521.

Taylor L.R. (1963). Analysis of the effects of temperature on insects in flight. *Journal of Animal Ecology*, **32**, 99-117.

Taylor L.R., French R.A. and Woiwood I.P. (1978). The Rothamsted insect survey and the urbanization of land in Great Britain. In *Perspectives in Urban Entomology* (Eds G.W. Frankie and C.S. Koehler), Academic Press, New York, pp31-65.

Thomas D.W. (1988). The distribution of bats in different ages of Douglas fir forests. *Journal of Wildlife Management*, **52**, 619-626.

Thomas D.W. and West S.D. (1991). Forest age associations of bats in the southern Washington Cascade and Oregon Coast Ranges. *U.S. Forest Service General Technical Report PNW*, **0 (285)**, 295-303.

Thomas D.W. and La Val R.K. (1988). Survey and census methods. In *Ecological and Behavioural Methods for the Study of Bats* (Ed. T.H. Kunz), Smithsonian Institution, Washington D.C., pp 77-89.

Thompson M.J.A. (1982). A common long-eared bat *Plecotus auritus*: moth predator-prey relationship. *Naturalist*, **107**, 87-97.

Tilling S.M. (1987). A key to the major groups of British terrestrial invertebrates. *Field Studies*, **6**, 695-766.

Tonkyn D.W. (1980). Formula for the volume sampled by a sweep net. *Annals of the Entomological Society of America*, **73**, 452-454.

Underhill G.W. (1940). Some factors influencing the feeding activities of simuliids in the field. *Journal Economic Entomology*, **33**, 915-917.

Unwin D.M. (1981). A key to the families of British Diptera. *Field Studies*, **5**, 513-553.

Unwin D.M. (1984). A key to the families of British beetles. *Field Studies*, **6**, 149-197.

Vaughan N. (1996). *Partitioning of foraging habitat resources among bats (Chiroptera) in Great Britain*. Ph.D. Thesis, University of Bristol.

Von Bartheld C.S. and Rubel E.W. (1989). Transient GABA-immunoreactivity in cranial nerves of the chick embryo. *Journal of Comparative Neurology*, **286**, 45-47.

Walsh A.L. and Mayle B.A. (1991). Bat activity in different habitats in a mixed lowland woodland. *Myotis*, **29**, 97-104.

Walsh A.L. and Harris S. (1996a). Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, **33**, 508-518.

Walsh A.L. and Harris S. (1996b). Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *Journal of Applied Ecology*, **33**, 519-529.

Walsh A.L., Harris S. and Hutson A.M. (1995). Abundance and habitat selection of foraging vespertilionid bats in Britain: a landscape-scale approach. *Symposium of the Zoological Society of London*, **67**, 325-344.

Waring P. (1988). Responses of moth populations to coppicing and the planting of conifers. In *Woodland Conservation and Research in the Clay*

Vale of Oxfordshire and Buckinghamshire (Eds K. Kirby and F.J. Wright). NCC, Peterborough. *Research and Survey in Nature Conservation* **15,** 82-113.

Waring P. (1989). Comparison of light-trap catches in deciduous and coniferous woodland habitats. *Entomologists Records (and Journal of Variation)*, **101,** 1-10.

Warwickshire Wildlife Trust (1983). *Tocil Wood Nature Reserve Draft Management Plan*, unpub.

Watkins L.C. (1972). A technique for monitoring the nocturnal activity of bats, with comments on the activity patterns of the evening bat, *Nycticeius humeralis. Transactions of the Kansas Academy of Science,* **74,** 261-268.

Webb P.I., Speakman J.R. and Racey P.A. (1994). Post-prandial urine loss and its relation to ecology in brown long-eared (*Plecotus auritus*) and Daubenton's (*Myotis daubentoni*) bats (Chiroptera: Vespertilionidae). *Journal of Zoology, Lond.*, **233,** 165-173.

Webb P.I., Speakman J.R. and Racey P.A. (1995). Evaporative water loss in two sympatric species of vespertilionid bat, *Plecotus auritus* and *Myotis daubentoni*: relation to foraging mode and implications for roost site selection. *Journal of Zoology, Lond.*, **235,** 269-278.

Wellington W.G. (1945). Conditions governing the distribution of insects in the free atmosphere. *The Canadian Entomologist*, **77,** 7-15.

Wiles G.J., Lemke T.O. and Payne N.H. (1989). Population estimates of fruit bats (*Pteropus mariannus*) in the Mariana Island. *Conservation Biology*, **3,** 66-76.

Wilkinson L., Hill M.A. and Vang E. (1992). *SYSTAT: Statistics*. SYSTAT, Illinois.

Williams C.B. (1939). An analysis of four years captures of insects in a light trap: Part I. General survey; sex proportion, phenology and time of

flight. *Transactions of the Royal Entomological Society of London*, **89**, 79-132.

Williams C.B. (1940). An analysis of four years captures of insects in a light trap: Part II. The effects of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. *Transactions of the Royal Entomological Society of London*, **90**, 227-306.

Wright A. (1990). British sawflies: a key to the adults of genera occurring in Britain. *Field Studies*, **7**, 531-593.

Yack J.E. (1988). Seasonal partitioning of atympate moths in relation to bat activity. *Canadian Journal of Zoology*, **66** (Notes), 753-755.

Yalden D.W. (1968). Neolithic bats from Dowel Cave, Derbyshire. *Journal of Zoology(A)*, **210**, 616-619.

Zar J.H. (1984). *Biostatistical Analysis*, 2nd Edition. Prentice-Hall International, New Jersey.

Zbinden K. (1989). Field observations on the flexibility of the acoustic behaviour of the northern bat *Nyctalus noctula* (Schreber 1774). *Revue Suisse de Zoologie*, **96**, 335-344.

Appendix I
1995 Insect Trap Catches

List of Abbreviations (used in Figs I.i - I.xii)

t = number of transects covered in one night

Ac = Acarina

Ar = Araneae

Op = Opiliones

Co = Coleoptera

De = Dermaptera

Di = Diptera

He = Hemiptera

Hy = Hymenoptera

Le = Lepidoptera

Ne = Neuroptera

Ps = Psocoptera

Tr = Trichoptera

Th = Thysanoptera

* (used in tables) indicates that the invertebrate was captured in larval form

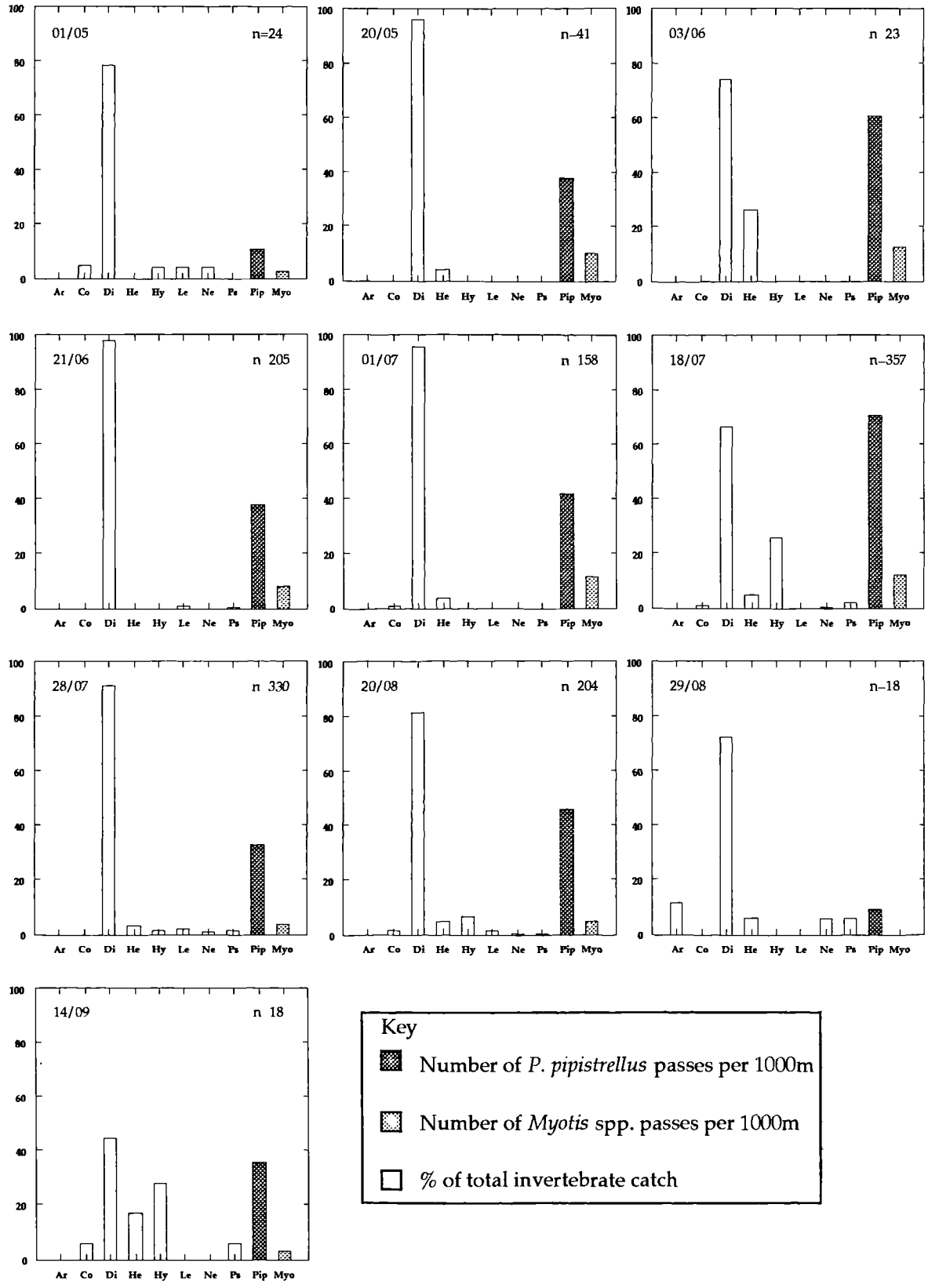


Fig I.i Bar charts showing changes in proportional abundance of different taxa in the suction trap throughout the season in Tocil Wood

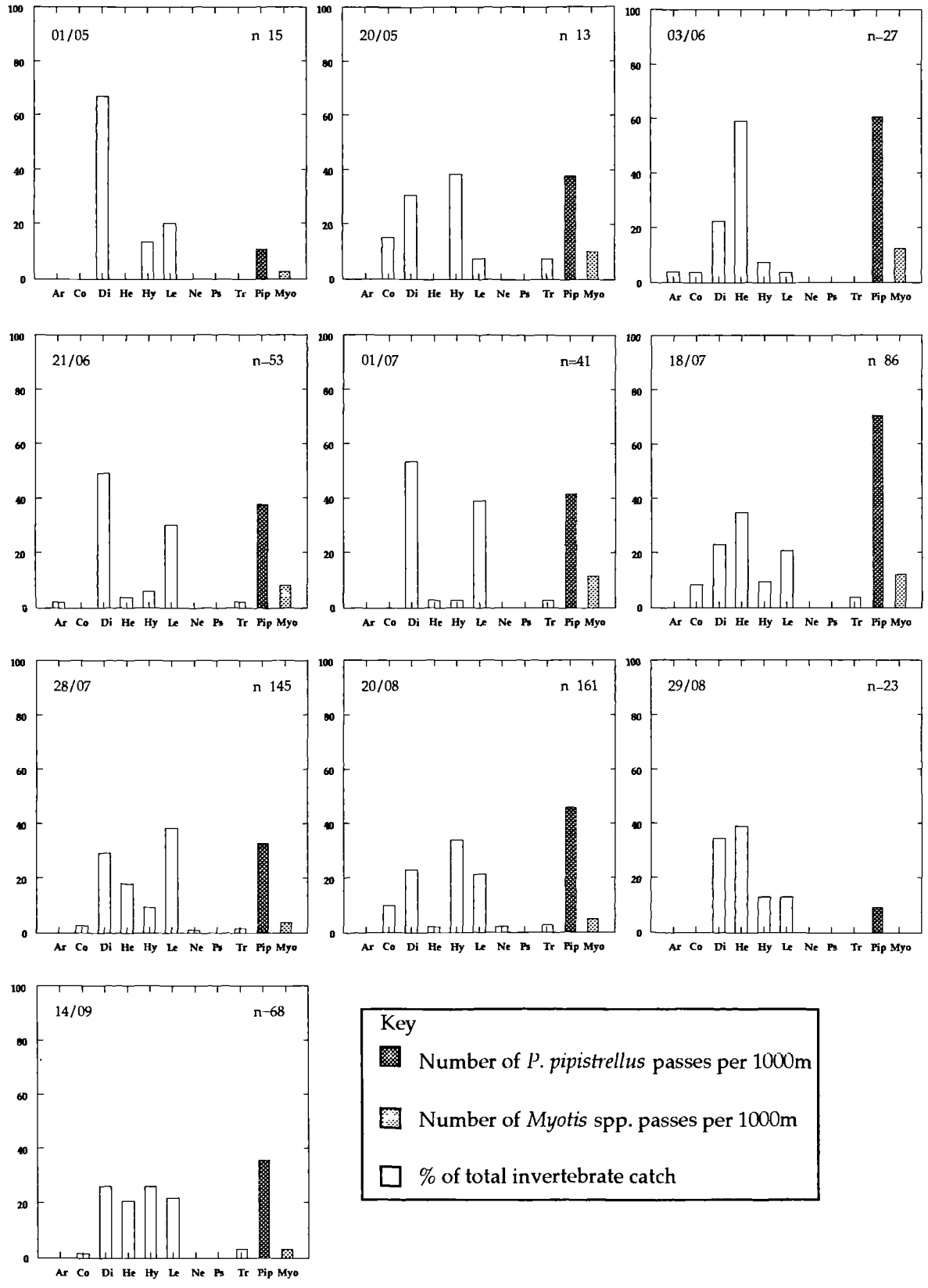


Fig I.ii Bar charts showing changes in proportional abundance of different taxa in the light trap throughout the season in Tocil Wood

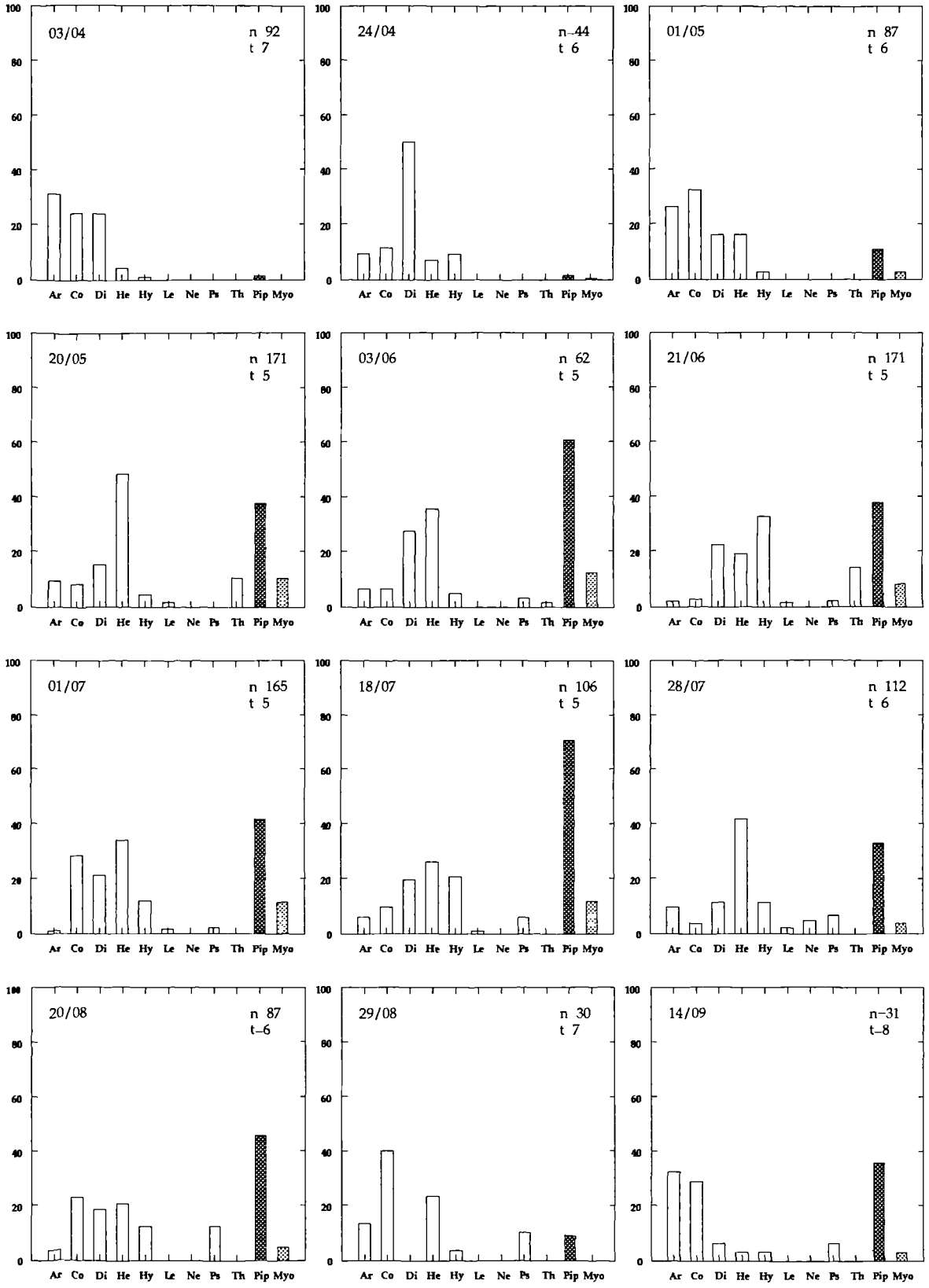


Fig I.iii Bar charts showing changes in proportional abundance of different taxa in the sweep net throughout the season in Tocil Wood

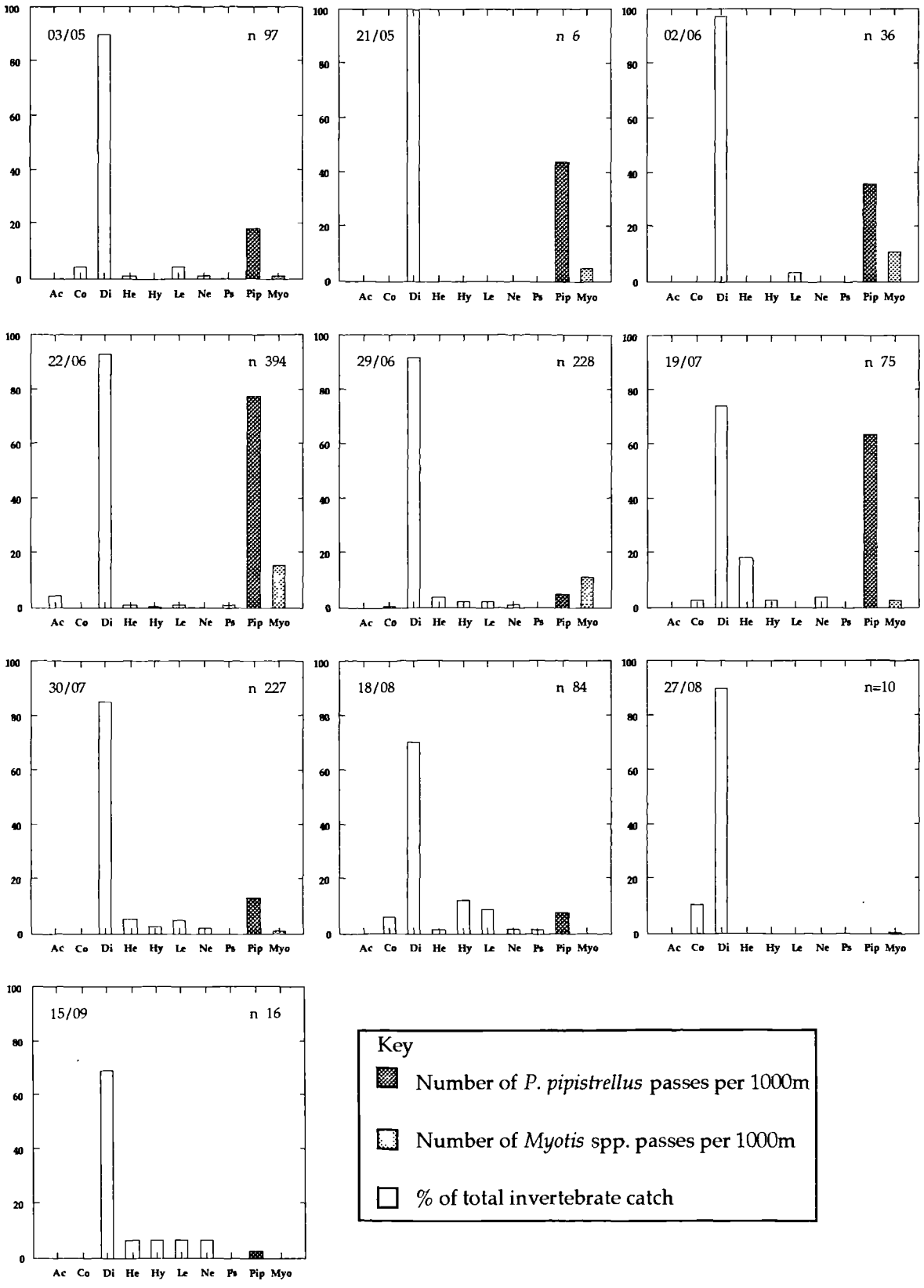


Fig I.iv Bar charts showing changes in proportional abundance of different taxa in the suction trap throughout the season in Roughknowles Wood

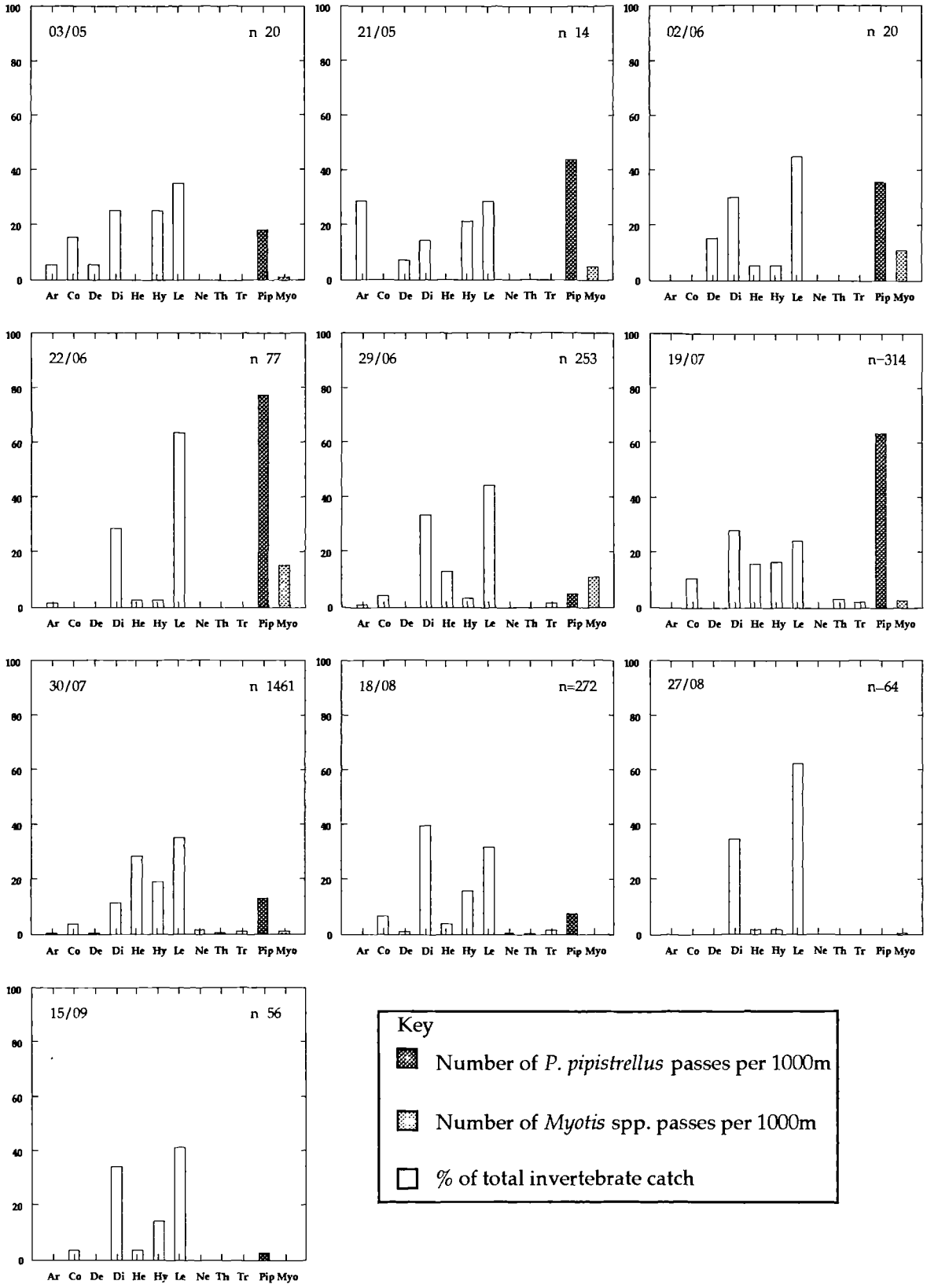


Fig I.v Bar charts showing changes in proportional abundance of different taxa in the light trap throughout the season in Roughknowles Wood

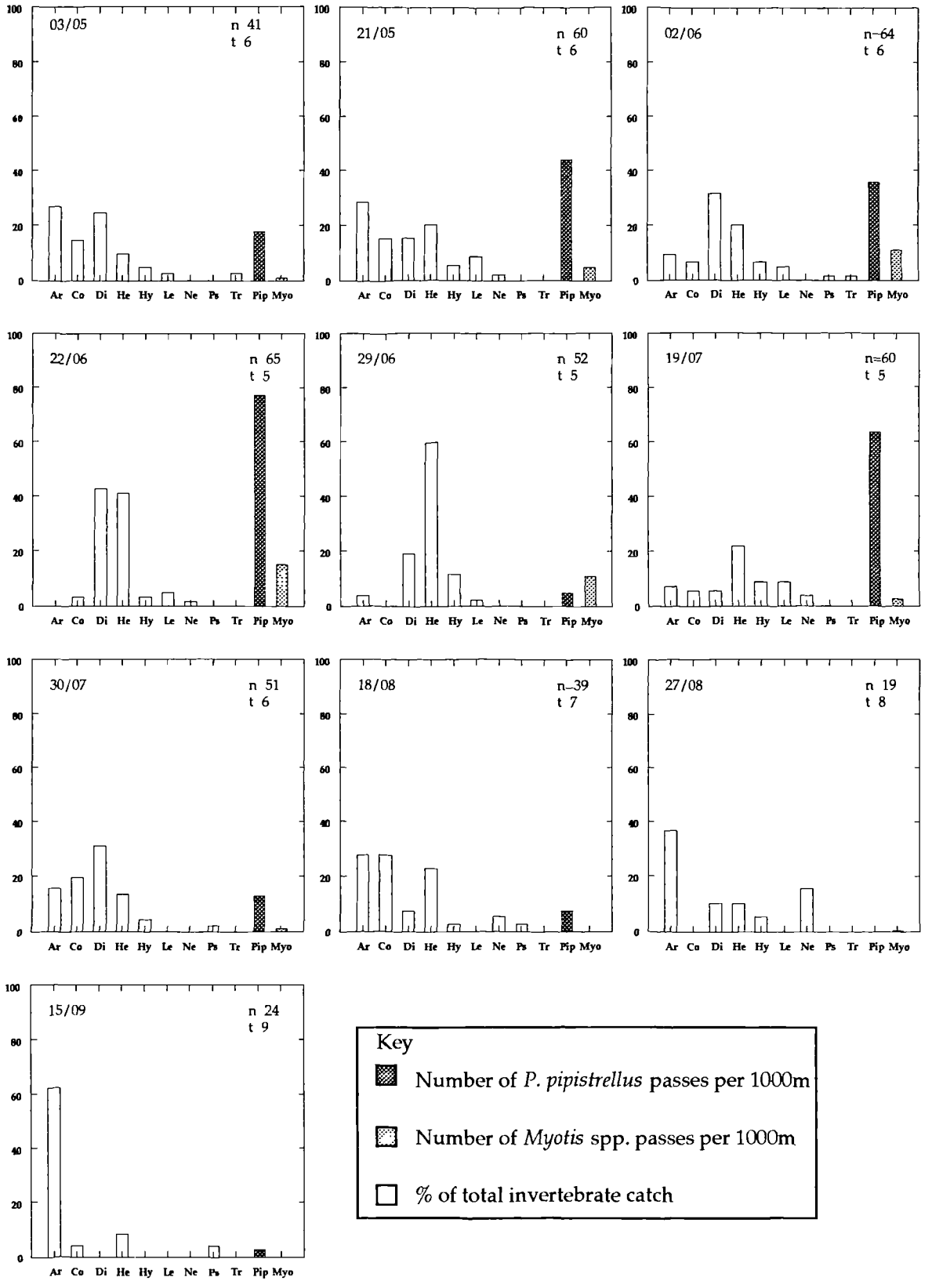


Fig I.vi Bar charts showing changes in proportional abundance of different taxa in the sweep net throughout the season in Roughknowles Wood

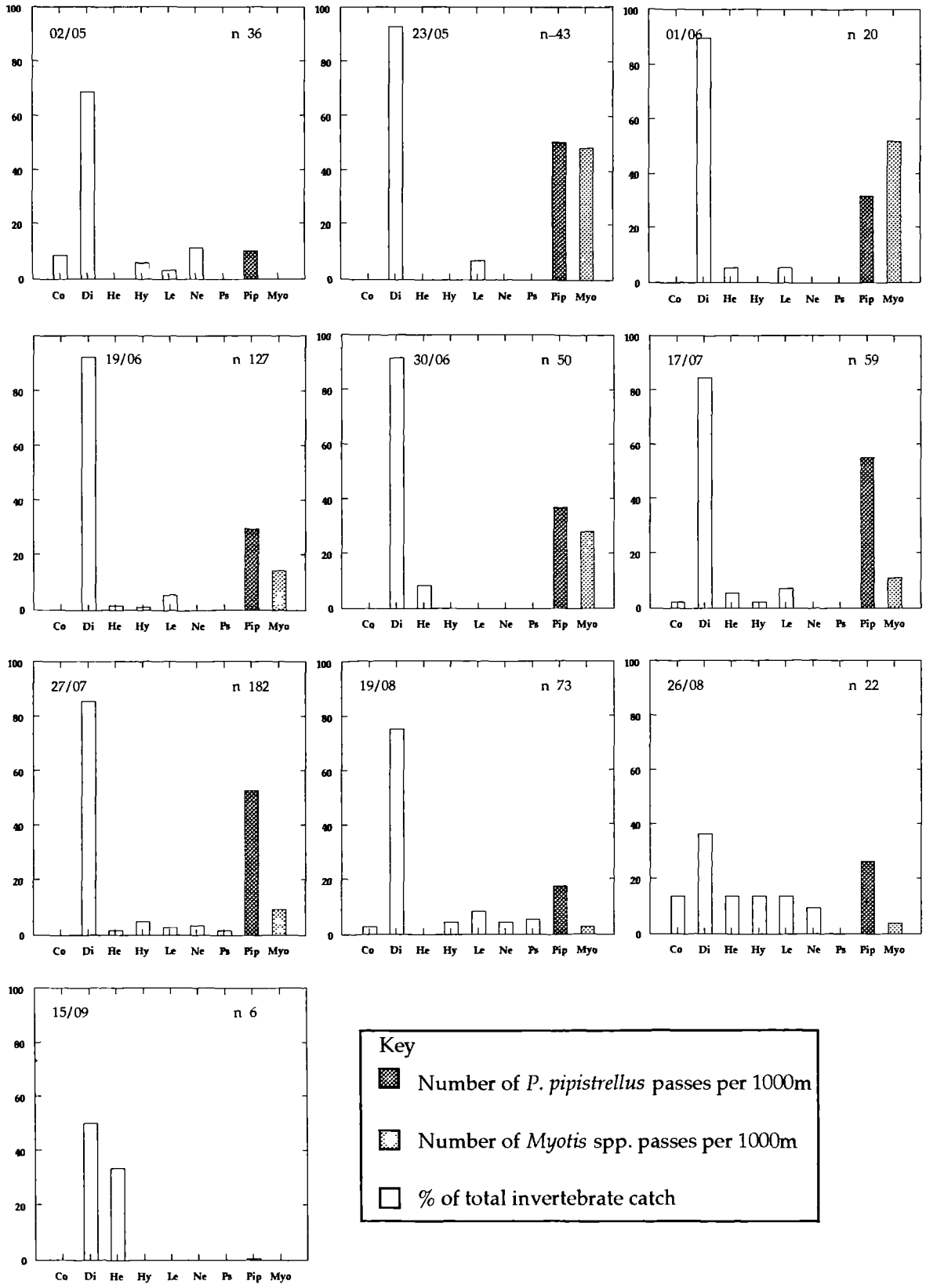


Fig I.vii Bar charts showing changes in proportional abundance of different taxa in the suction trap throughout the season in Chase Wood

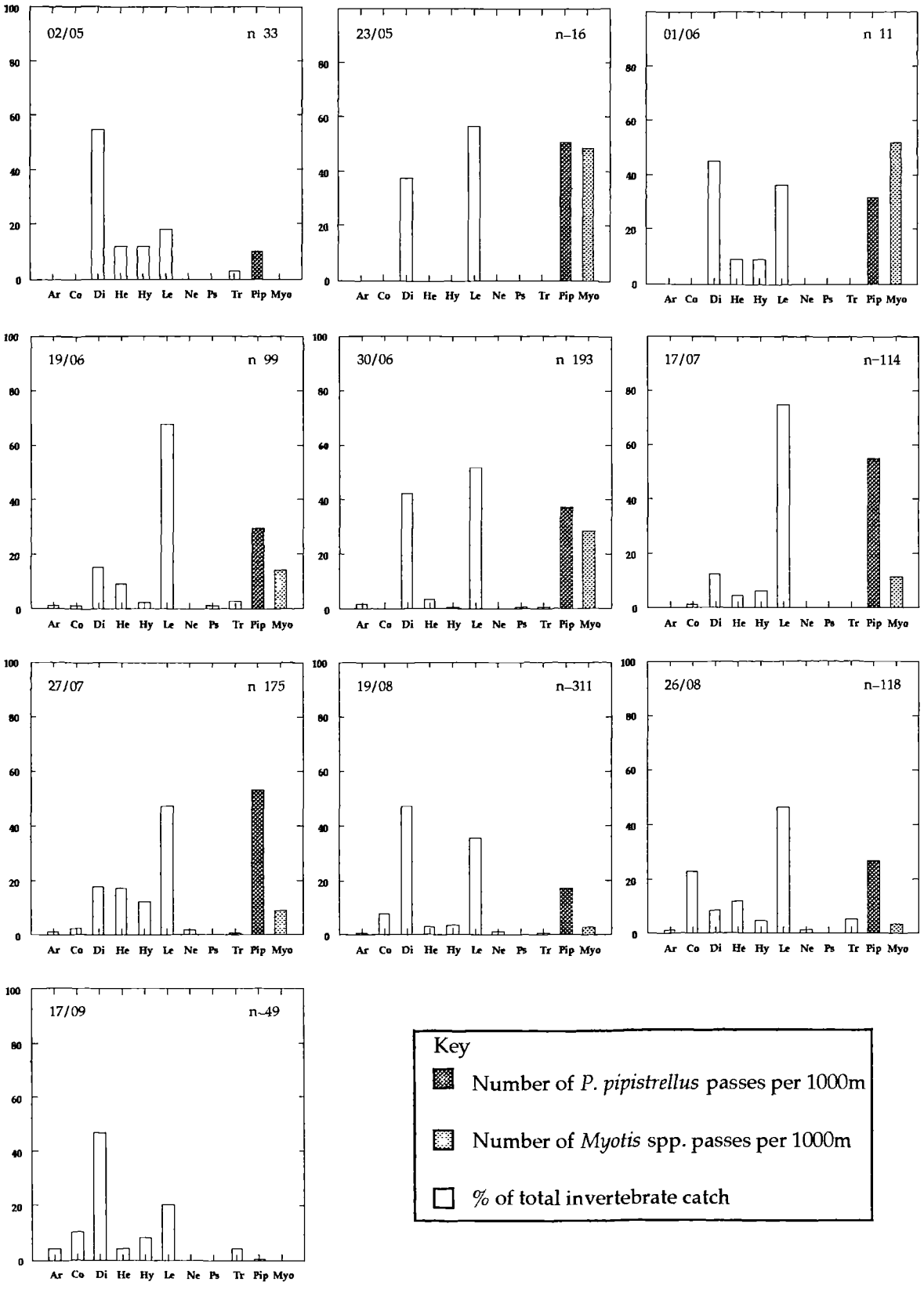


Fig I.viii Bar charts showing changes in proportional abundance of different taxa in the light trap throughout the season in Chase Wood

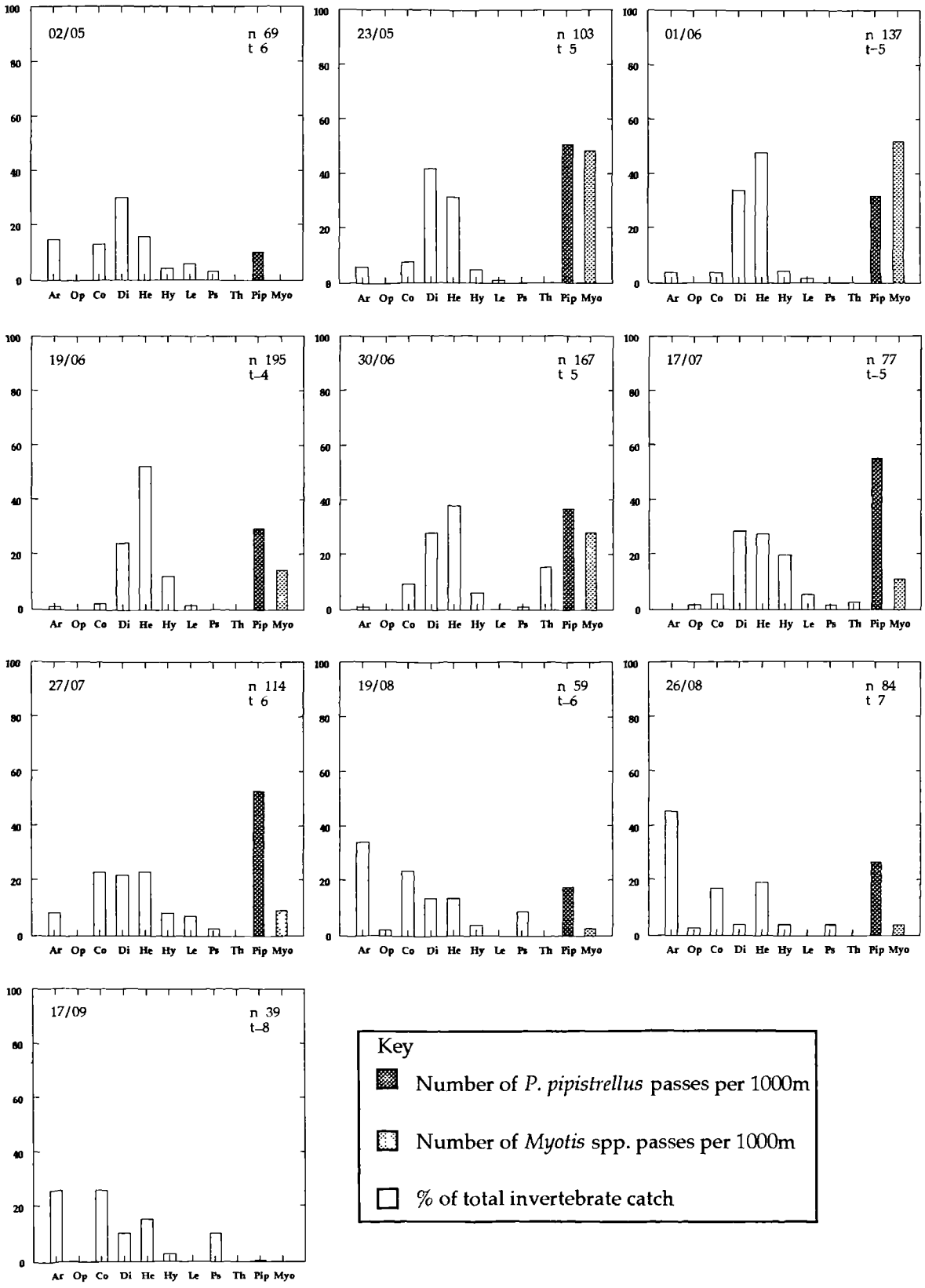


Fig I.ix Bar charts showing changes in proportional abundance of different taxa in the sweep net throughout the season in Chase Wood

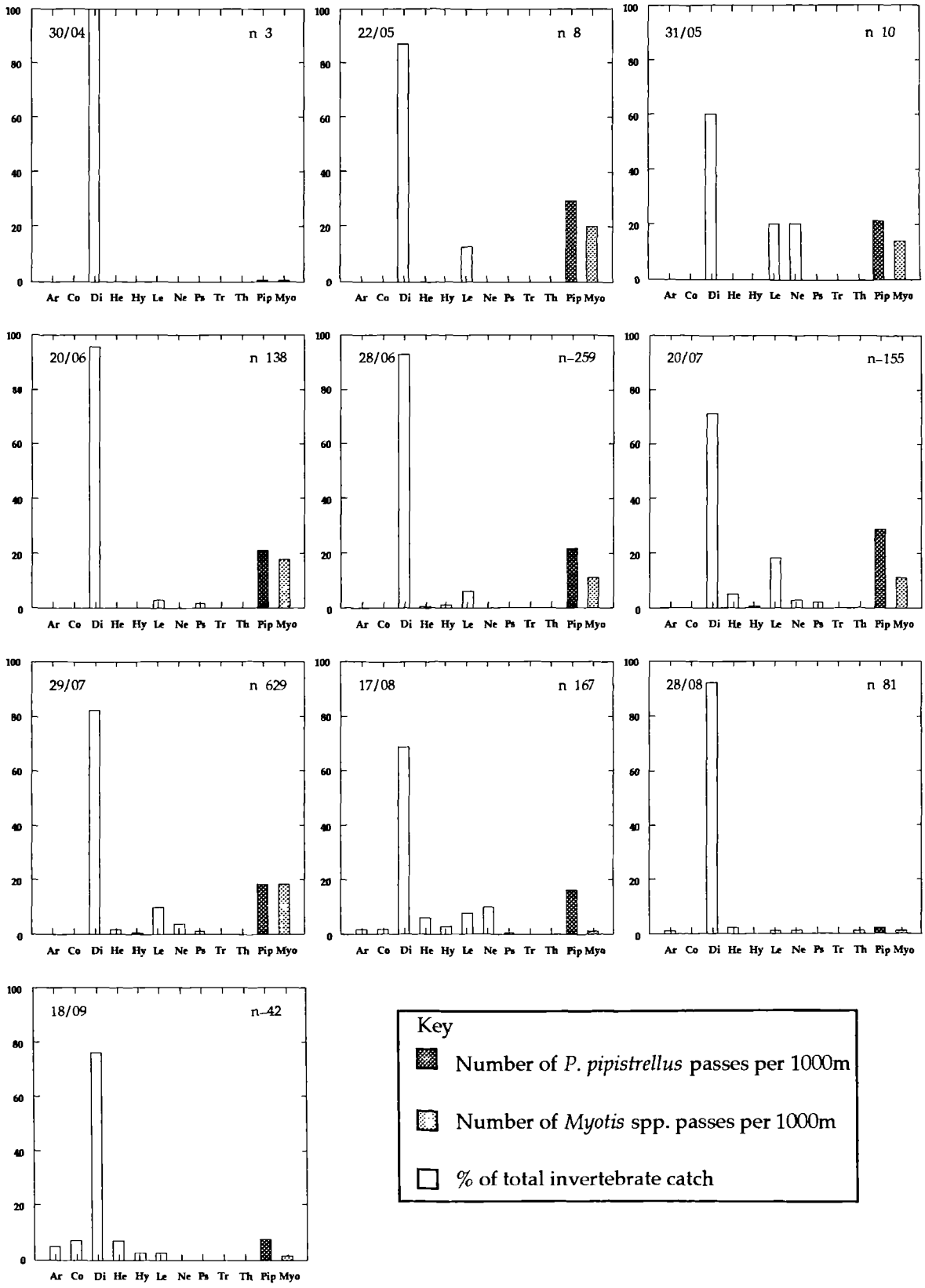


Fig I.x Bar charts showing changes in proportional abundance of different taxa in the suction trap throughout the season in Long Itchington Wood

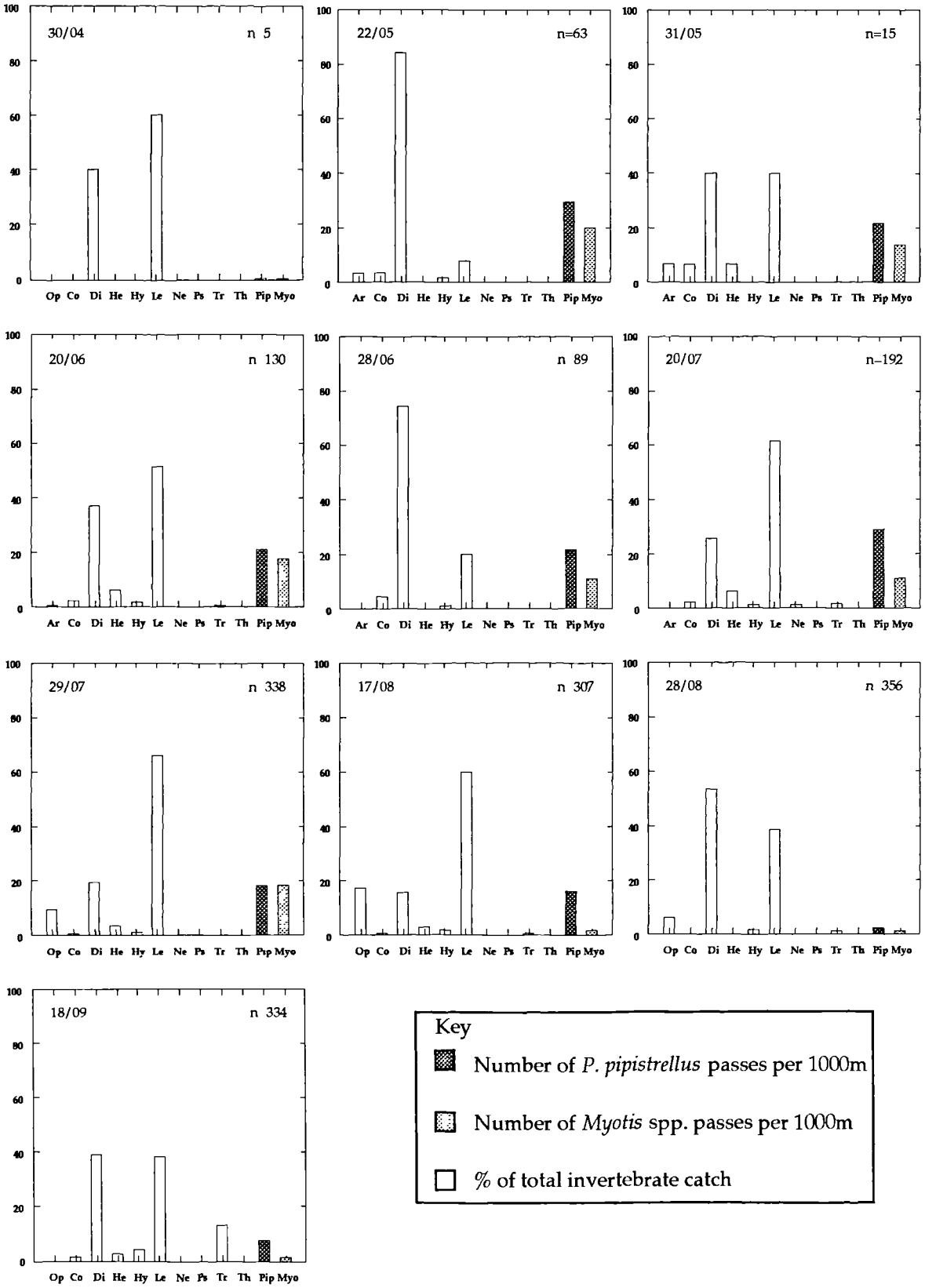


Fig I.xi Bar charts showing changes in proportional abundance of different taxa in the light trap throughout the season in Long Itchington Wood

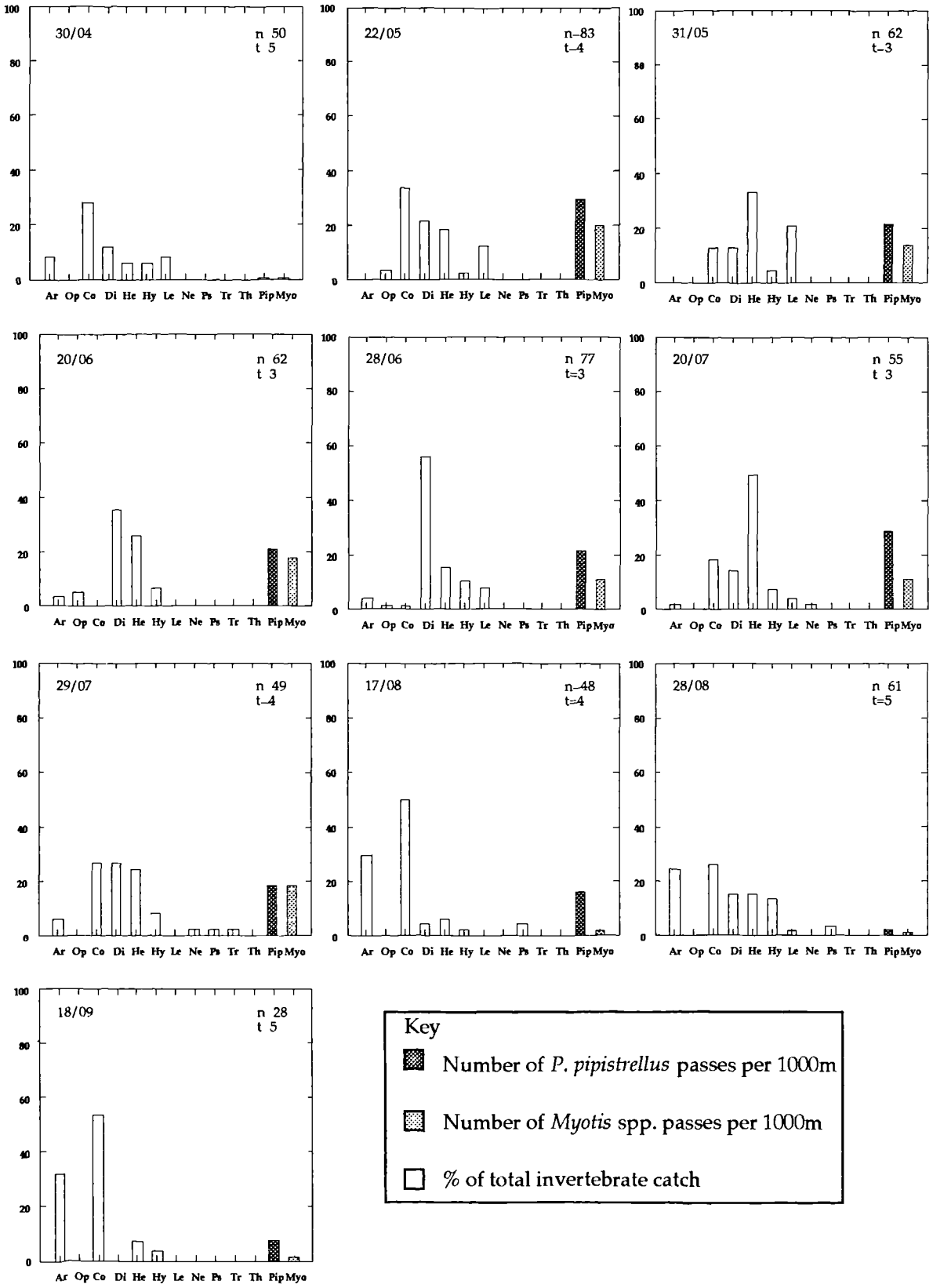


Fig I.xii Bar charts showing changes in proportional abundance of different taxa in the sweep net throughout the season in Long Itchington Wood

Appendix I: Tocil Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arachnida	Acarina			3	0.21
	Araneae		Metidae	1	0.07
			Tetragnathidae	1	0.07
Insecta	Coleoptera		Chrysomelidae	1	0.07
			Lathridiidae	3	0.21
			Nitidulidae	1	0.07
	Coleoptera		Staphylinidae	4	0.29
	Diptera		Trichoceridae	1	0.07
			Chaoboridae	1	0.07
			Ceratopogonidae	45	3.21
			Cecidomyiidae	808	57.67
			Chironomidae	70	5.00
			Culicidae	4	0.29
			Diastatidae	1	0.07
			Drosophilidae	5	0.36
			Ectopsocidae	1	0.07
			Empididae	3	0.21
			Ephydridae	1	0.07
			Lauxaniidae	1	0.07
			Lonchopteridae	2	0.14
			Milichidae	1	0.07
			Muscidae	3	0.21
			Mycetophilidae	2	0.14
			Phoridae	2	0.14
			Psychodidae	220	15.70
			Sarcophagidae	2	0.14
			Scatopsidae	5	0.36
			Simulidae	2	0.14
			Tachinidae	1	0.07
			Tipulidae	2	0.14
			Trichoceridae	1	0.07
	Hemiptera	Aphidoidea		45	3.21
			Adelgidae	1	0.07
			Cicadellidae	2	0.14
			Cimicidae	3	0.21
			Miridae	3	0.21
			Psyllidae	1	0.07
	Hymenoptera	Chalcidoidea		5	0.36
		Ichneumonoidea		59	4.21
			Braconidae	24	1.71
			Cynipidae	2	0.14
			Ichneumonidae	3	0.21
			Pteromalidae	7	0.50
			Tenthredinidae	1	0.07
			Torymidae	9	0.64
			Trichogrammitidae	2	0.14
	Lepidoptera	Micropterigoidea		2	0.14

Appendix I: Tocil Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
		Pyraloidea		1	0.07
		Tineoidea		3	0.21
			Geometridae	2	0.14
			Noctuidae	1	0.07
			Pyralidae	2	0.14
			Tortricidae	1	0.07
		Microlepidoptera		2	0.14
	Neuroptera		Chrysopidae	7	0.50
	Psocoptera		Ectopsocidae	14	1.00
			Troctidae	1	0.07
				1401	100.00

Appendix I: Tocil Wood, Light Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arachnida	Acarina			3	0.45
	Araneae		Araneidae	1	0.15
			Gnaphosidae	1	0.15
			Linyphidae	1	0.15
Insecta	Collembola	Entomobryoidea		1	0.15
	Coleoptera		Carabidae	1	0.15
			Chrysomelidae	3	0.45
			Cisidae	1	0.15
			Coccinellidae	2	0.30
			Dermestidae	1	0.15
			Elateridae	3	0.45
			Haliplidae	5	0.75
			Heteroceridae	3	0.45
			Lathridiidae	6	0.90
			Nitidulidae	1	0.15
			Scarabaeidae	6	0.90
			Scaphidiidae	1	0.15
	Dermaptera		Forficulidae	1	0.15
	Diptera		Agromyzidae	6	0.90
			Anthomyiidae	11	1.65
			Anisopodidae	2	0.30
			Calliphoridae	2	0.30
			Ceratopogonidae	4	0.60
			Cecidomyiidae	18	2.70
			Chironomidae	69	10.36
			Chloropidae	2	0.30
			Chamaemyiidae	1	0.15
			Clusiidae	1	0.15
			Culicidae	3	0.45
			Dolichopodidae	2	0.30
			Drosophilidae	2	0.30
			Dryomyzidae	2	0.30
			Empididae	39	5.86
			Fanniidae	7	1.05
			Lauxaniidae	3	0.45
			Lonchopteridae	1	0.15
			Mycetophilidae	11	1.65
			Opomyzidae	2	0.30
			Phoridae	5	0.75
			Psychodidae	2	0.30
			Rhagionidae	1	0.15
			Sciaridae	3	0.45
			Scatopsidae	1	0.15
			Simulidae	2	0.30
			Sphaeroceridae	3	0.45
			Stratiomyidae	1	0.15
			Syrphidae	1	0.15

Appendix I: Tocil Wood, Light Trap Catches

Class	Order	Superfamily	Family	No.	% Total
			Tipulidae	17	2.55
	Hemiptera	Aphidoidea		78	11.71
			Acanthosomidae	1	0.15
			Cicadellidae	14	2.10
			Cimicidae	2	0.30
			Corixidae	2	0.30
			Delphacidae	1	0.15
			Miridae	2	0.30
			Psyllidae	1	0.15
	Hymenoptera	Chalcidoidea		33	4.95
		Proctotrupoidea		5	0.75
			Braconidae	21	3.15
			Cynipidae	13	1.95
			Diprionidae	1	0.15
			Formicidae	2	0.30
			Ichneumonidae	32	4.80
			Tenthredinidae	3	0.45
			Vespidae	1	0.15
	Lepidoptera	Microlepidoptera		9	1.35
		Pyraloidea		13	1.95
		Tineoidea		9	1.35
			Arctiidae	2	0.30
			Eriocranidae	3	0.45
			Geometridae	*12*	*1.80*
			Incurvariidae	3	0.45
			Noctuidae	92	13.81
			Pyralidae	14	2.10
			Tortricidae	12	1.80
	Neuroptera		Coniopterygidae	1	0.15
			Hemerobiidae	1	0.15
			Sisyridae	2	0.30
	Thysanoptera		Phlaeothripidae	1	0.15
			Thripidae	1	0.15
	Trichoptera		Baetidae	3	0.45
			Hydropsychidae	2	0.30
			Limnephilidae	6	0.90
			Sericostomatidae	3	0.45
				666	100.00

Appendix I: Tocil Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.		% Total
Arachnida	Acarina			6		0.51
	Araneae		Araneidae	27		2.28
			Clubionidae	5		0.42
			Dictynidae	4		0.34
			Gnaphosidae	4		0.34
			Linyphidae	13		1.10
			Liocranidae	1		0.08
			Metidae	38		3.21
			Tetragnathidae	14		1.18
			Theridiidae	11		0.93
		Unidentified		3		0.25
	Opiliones		Phalangiidae	9		0.76
		Unidentified		1		0.08
Crustacea	Chilopoda			1		0.08
	Isopoda			1		0.08
Insecta	Collembola	Entomobryoidea		58		4.90
			Sminthuridae	5		0.42
	Coleoptera		Anobiidae	1		0.08
			Byturidae	1		0.08
			Carabidae	8		0.68
			Cantharidae	1		0.08
			Cerambycidae	2		0.17
			Chrysomelidae	48		4.05
			Coccinellidae	19		1.60
			Colydidae	1		0.08
			Cucijidae	1		0.08
			Elateridae	4		0.34
			Endomychiidae	3		0.25
			Lathridiidae	8		0.68
			Lampyridae	1		0.08
			Leiobidae	2		0.17
			Lymexylidae	2		0.17
			Melandryidae	3		0.25
			Nitidulidae	58		4.90
			Staphylinidae	13		1.10
		Unidentified		5		0.42
				1	*	0.08
	Dermaptera		Forficulidae	5		0.42
	Diptera		Agromyzidae	17		1.44
			Anthomyiidae	5		0.42
			Anisopodidae	1		0.08
			Asteiidae	1		0.08
			Aulacigastridae	2		0.17
			Ceratopogonidae	1		0.08
			Cecidomyiidae	42		3.55
			Chironomidae	47		3.97
			Chloropidae	12		1.01

Appendix I: Tocil Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.		% Total
			Torymidae	5		0.42
	Lepidoptera	Microlepidoptera		3		0.25
		Tineoidea		1		0.08
			Geometridae	2		0.17
			Incurvariidae	1		0.08
			Pteriphoridae	1		0.08
				1	*	0.08
		Unidentified		1		0.08
	Neuroptera		Chrysopidae	5		0.42
	Psocoptera		Caecilidae	3		0.25
			Ectopsocidae	24		2.03
			Epipsocidae	4		0.34
			Mesopsocidae	1		0.08
			Peripsocidae	1		0.08
			Psyllipsocidae	2		0.17
			Stenopsocidae	4		0.34
	Thysanoptera		Phlaethripidae	42		3.55
			Thripidae	1		0.08
	Trichoptera		Hydroptilidae	1		0.08
				1184		100.00

Appendix I: Roughknowles Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arachnida	Acarina			16	1.25
	Arachnida		Linyphidae	1	0.08
				1	0.08
Insecta	Coleoptera		Carabidae	1	0.08
			Chrysomelidae	3	0.23
			Coccinellidae	2	0.16
			Cryptophagidae	1	0.08
			Lathridiidae	1	0.08
			Nitidulidae	4	0.31
			Scratiidae	1	0.08
	Diptera	Unidentified		1	0.08
			Agromyzidae	1	0.08
			Asteiidae	1	0.08
			Bibionidae	2	0.16
			Ceratopogonidae	7	0.54
			Cecidomyiidae	543	42.26
			Chironomidae	50	3.89
			Culicidae	1	0.08
			Dixidae	1	0.08
			Drosophilidae	1	0.08
			Empididae	1	0.08
			Mycetophilidae	5	0.39
			Phoridae	1	0.08
			Psychodidae	503	39.14
			Scatopsidae	3	0.23
			Sphaeroceridae	2	0.16
			Tipulidae	1	0.08
	Hemiptera	Aphidoidea		39	3.04
			Cicadellidae	5	0.39
			Miridae	1	0.08
			Nabiidae	1	0.08
			Psyllidae	1	0.08
	Hymenoptera	Chalcidoidea		16	1.25
		Proctotrupoidea		1	0.08
			Braconidae	6	0.47
			Cynipidae	1	0.08
			Formicidae	2	0.16
			Pteromalidae	1	0.08
	Lepidoptera	Microlepidoptera		7	0.54
		Pyraloidea		1	0.08
		Tineoidea		19	1.48
			Geometridae	2	0.16
			Nepticulidae	1	0.08
			Noctuidae	2	0.16
			Tortricidae	4	0.31
	Neuroptera		Chrysopidae	13	1.01
			Coniopterygidae	2	0.16

Appendix I: Roughknowles Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
			Sisyridae	1	0.08
	Psocoptera		Caecilidae	3	0.23
			Elipsocidae	1	0.08
				1285	100.00

Appendix I: Roughknowles Wood, Light Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arachnida	Araneae		Araneidae	1	0.04
			Gnaphosidae	2	0.08
			Linyphidae	2	0.08
			Liocranidae	1	0.04
			Theridiidae	3	0.12
Insecta	Collembola	Entomobryoidea		1	0.04
	Coleoptera		Anobiidae	1	0.04
			Carabidae	38	1.47
			Cantharidae	17	0.66
			Chrysomelidae	1	0.04
			Coccinellidae	3	0.12
			Cryptophagidae	8	0.31
			Curculionidae	3	0.12
			Dermestidae	7	0.27
			Elateridae	3	0.12
			Haliplidae	4	0.15
			Heteroceridae	7	0.27
			Lathridiidae	1	0.04
			Leiobidae	1	0.04
			Melandryidae	6	0.23
			Mycetophilidae	2	0.08
			Scarabaeidae	13	0.50
			Scirtidae	1	0.04
			Silphidae	1	0.04
			Staphylinidae	1	0.04
	Dermaptera		Forficulidae	12	0.46
	Diptera		Agromyzidae	1	0.04
			Anthomyiidae	40	1.55
			Bibionidae	4	0.15
			Cecidomyiidae	28	1.08
			Chironomidae	301	11.64
			Chloropidae	6	0.23
			Culicidae	7	0.27
			Dolichopodidae	5	0.19
			Empididae	63	2.44
			Ephydridae	3	0.12
			Fanniidae	2	0.08
			Muscidae	16	0.62
			Mycetophilidae	17	0.66
			Phyrganeidae	1	0.04
			Phoridae	2	0.08
			Psychodidae	5	0.19
			Sarcophagidae	1	0.04
			Sciaridae	5	0.19
			Scatophagidae	4	0.15
			Scatopsidae	7	0.27
			Sepsidae	1	0.04

Appendix I: Roughknowles Wood, Light Trap Catches

Class	Order	Superfamily	Family	No.	% Total
			Sphaeroceridae	2	0.08
			Stratiomyidae	1	0.04
			Tipulidae	24	0.93
	Ephemeroptera		Baetidae	2	0.08
	Hemiptera	Aphidoidea		463	17.90
			Cicadellidae	16	0.62
			Cimicidae	1	0.04
			Corixidae	24	0.93
			Delphacidae	2	0.08
			Miridae	12	0.46
			Psyllidae	1	0.04
	Hymenoptera	Chalcidoidea		28	1.08
			Braconidae	39	1.51
			Cynipidae	19	0.73
			Formicidae	265	10.24
			Ichneumonidae	44	1.70
			Tenthredinidae	1	0.04
			Vespidae	2	0.08
	Lepidoptera	Incurvariidae		2	0.08
		Microlepidoptera		262	10.13
		Pyraloidea		51	1.97
		Tineoidea		*40*	*1.55*
			Arctiidae	46	1.78
			Drepanidae	2	0.08
			Geometridae	45	1.74
			Lasiocmpidae	3	0.12
			Lymantriidae	4	0.15
			Nepticulidae	1	0.04
			Noctuidae	424	16.39
			Oecophoridae	2	0.08
			Pyralidae	21	0.81
			Tortricidae	22	0.85
			Yponomeutidae	1	0.04
	Neuroptera		Chrysopidae	1	0.04
			Coniopterygidae	1	0.04
			Sisyridae	18	0.70
	Psocoptera		Mesopsocidae	1	0.04
	Thysanoptera		Thripidae	13	0.50
	Trichoptera		Beraeidae	3	0.12
			Hydropsychidae	16	0.62
			Limnephilidae	2	0.08
			Phyrganeidae	1	0.04
				2587	100.00

Appendix I: Roughknowles Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
Arachnida	Acarina			1		0.20
	Araneae		Araneidae	20		4.02
			Clubionidae	3		0.60
			Gnaphosidae	4		0.80
			Linyphidae	17		3.41
			Liocranidae	2		0.40
			Metidae	16		3.21
			Tetragnathidae	3		0.60
			Theridiidae	19		3.82
			Thomisidae	1		0.20
	Opiliones		Phalangiidae	4		0.80
Crustacea	Isopoda			2		0.40
Insecta	Collembola	Entomobryoidea		49		9.84
	Coleoptera		Attelabidae	1		0.20
			Cantharidae	1		0.20
			Chrysopidae	5		1.00
			Chrysomelidae	6		1.20
			Coccinellidae	9		1.81
			Curculionidae	3		0.60
			Elateridae	5		1.00
			Lathridiidae	4		0.80
			Nitidulidae	6		1.20
			Staphylinidae	5		1.00
				1	*	0.20
	Dermaptera		Forficulidae	3		0.60
			Labiidae	1		0.20
	Diptera		Agromyzidae	21		4.22
			Anthomyiidae	2		0.40
			Bibionidae	3		0.60
			Ceratopogonidae	1		0.20
			Cecidomyiidae	16		3.21
			Chironomidae	5		1.00
			Chloropidae	3		0.60
			Chamaemyiidae	1		0.20
			Clusiidae	1		0.20
			Empididae	10		2.01
			Lauxaniidae	6		1.20
			Lonchopteridae	4		0.80
			Muscidae	3		0.60
			Mycetophilidae	2		0.40
			Opomyzidae	8		1.61
			Psychodidae	14		2.81
			Sarcophagidae	1		0.20
			Sciaridae	1		0.20
			Scatophagidae	3		0.60
			Sepsidae	7		1.41
			Sphaeroceridae	1		0.20

Appendix I: Roughknowles Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
			Syrphidae	3		0.60
			Tipulidae	1		0.20
	Hemiptera	Aphidoidea		68		13.65
			Cicadellidae	6		1.20
			Cimicidae	3		0.60
			Delphacidae	4		0.80
			Miridae	22		4.42
			Nabiidae	8		1.61
		Unidentified		9		1.81
	Hymenoptera	Chalcidoidea		9		1.81
			Platygasteridae	2		0.40
		Proctotrupoidea		1		0.20
			Braconidae	3		0.60
			Cynipidae	7		1.41
			Formicidae	2		0.40
			Ichneumonidae	5		1.00
			Platygasteridae	1		0.20
			Pteromalidae	2		0.40
			Tenthredinidae	2		0.40
	Lepidoptera	Incurvaroidea		4		0.80
		Tineoidea		1		0.20
			Geometridae	1		0.20
			Nepticulidae	2		*0.40*
			Noctuidae	3		0.60
			Tortricidae	3		0.60
			Yponomeutidae	1		0.20
				2	*	0.40
		Unidentified		1		0.20
	Neuroptera		Chrysopidae	8		1.61
			Hemerobiidae	2		0.40
				1	*	0.20
	Psocoptera		Caecilidae	1		0.20
			Ectopsocidae	*2*		*0.40*
			Mesopsocidae	1		0.20
	Thysanoptera		Thripidae	1		0.20
	Trichoptera		Limnephilidae	2		0.40
				498		100.00

Appendix I: Chase Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arach	Acarina			1	0.16
	Aran		Gnaphosidae	1	0.16
Insecta	Coleoptera		Chrysomelidae	1	0.16
			Lathridiidae	6	0.97
			Nitidulidae	1	0.16
			Staphylinidae	1	0.16
	Diptera		Agromyzidae	2	0.32
			Anisopodidae	1	0.16
			Ceratopogonidae	13	2.10
			Cecidomyiidae	345	55.74
			Chironomidae	25	4.04
			Drosophilidae	2	0.32
			Empididae	1	0.16
			Mycetophilidae	5	0.81
			Psychodidae	117	18.90
			Ptilidae	1	0.16
			Sciaridae	1	0.16
			Scatopsidae	1	0.16
			Sphaeroceridae	1	0.16
			Tipulidae	3	0.48
	Hemiptera	Aphidoidea		10	1.62
			Cercopidae	1	0.16
			Cicadellidae	4	0.65
			Cixiidae	1	0.16
			Miridae	2	0.32
	Hymenoptera	Chalcidoidea		8	1.29
		Ichneumonoidea		1	0.16
			Braconidae	6	0.97
			Cynipidae	1	0.16
			Ichneumonidae	2	0.32
			Platygasteridae	1	0.16
	Lepidoptera	Microlepidoptera		1	0.16
		Nepticuloidea		4	0.65
		Pryraloidea		2	0.32
		Tineoidea		14	2.26
			Geometridae	1	0.16
			Incurvariidae	1	0.16
			Nepticulidae	2	0.32
			Noctuidae	4	0.65
			unidentified	1	0.16
			Pyralidae	1	0.16
	Neuroptera		Chrysopidae	15	2.42
	Psocoptera		Caecilidae	2	0.32
			Ectopsocidae	5	0.81
				619	100.00

Appendix I: Chase Wood, Light Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arachnida	Araneae		Gnaphosidae	2	0.18
			Linyphidae	4	0.35
			Metidae	1	0.09
			Tetragnathidae	3	0.26
			Theridiidae	1	0.09
	Opiliones		Phalangiidae	2	0.18
		Unidentified		1	0.09
Insecta	Collembola		Entomobryoidea	2	0.18
	Coleoptera		Carabidae	3	0.26
			Chrysomelidae	2	0.18
			Dermestidae	1	0.09
			Haliplidae	3	0.26
			Heteroceridae	8	0.71
			Lathridiidae	7	0.62
			Nitidulidae	1	0.09
			Scarabaeidae	35	3.09
			Silphidae	3	0.26
	Dermaptera		Forficulidae	3	0.26
			Agromyzidae	14	1.24
			Anthomyiidae	8	0.71
			Anisopodidae	3	0.26
			Bibionidae	2	0.18
			Ceratopogonidae	3	0.26
			Cecidomyiidae	64	5.65
			Chironomidae	134	11.83
			Chloropidae	1	0.09
			Chamaemyiidae	1	0.09
			Dolichopodidae	4	0.35
			Drosophilidae	2	0.18
			Empididae	10	0.88
			Fanniidae	1	0.09
			Lauxaniidae	1	0.09
			Lonchopteridae	5	0.44
			Muscidae	5	0.44
			Mycetophilidae	16	1.41
			Opomyzidae	4	0.35
			Phoridae	2	0.18
			Pipunculidae	1	0.09
			Psychodidae	10	0.88
			Rhagionidae	5	0.44
			Sciaridae	1	0.09
			Scatophagidae	1	0.09
			Scatopsidae	1	0.09
			Sphaeroceridae	2	0.18
			Tipulidae	49	4.32
			Trichoceridae	1	0.09
	Ephemeroptera		Baetidae	2	0.18

Appendix I: Chase Wood, Light Trap Catches

Class	Order	Superfamily	Family	No.	% Total
	Hemiptera	Aphidoidea		8	0.71
			Acanthosomidae	6	0.53
			Cercopidae	3	0.26
			Cicadellidae	49	4.32
			Corixidae	4	0.35
			Delphacidae	2	0.18
			Miridae	4	0.35
			Pentatomidae	3	0.26
			Tenthredinidae	1	0.09
	Hymenoptera	Chalcidoidea		4	0.35
		Proctotrupoidea		1	0.09
			Braconidae	11	0.97
			Cynipidae	9	0.79
			Ichneumonidae	25	2.21
			Tenthredinidae	5	0.44
	Lepidoptera	Micropterigoidea		1	0.09
		Microlepidoptera		103	9.09
		Pyraloidea		61	5.38
		Tineoidea		23	2.03
			Arctiidae	10	0.88
			Eriocranidae	1	0.09
			Geometridae	84	7.41
			Lasiocampidae	1	0.09
			Lymantriidae	6	0.53
			Noctuidae	224	19.77
			Notodontidae	4	0.35
			Oecophoridae	1	0.09
			Pyralidae	1	0.09
			Thyatiridae	1	0.09
			Tortricidae	17	1.50
			Yponomeutidae	1	0.09
	Neuroptera		Coniopterygidae	1	0.09
			Sisyridae	6	0.53
	Psocoptera		Mesopsocidae	1	0.09
			Peripsocidae	1	0.09
	Trichoptera		Baetidae	4	0.35
			Limnephilidae	4	0.35
			Molannidae	1	0.09
			Phyrganeidae	3	0.26
			Philopotamitidae	1	0.09
			Sericostomatidae	2	0.18
				1133	100.00

Appendix I: Chase Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
Arachnida	Acarina			2		0.18
	Araneae		Araneidae	19		1.71
			Clubionidae	5		0.45
			Gnaphosidae	1		0.09
			Linyphidae	34		3.06
			Metidae	25		2.25
			Philodromidae	1		0.09
			Tetragnathidae	16		1.44
			Theridiidae	10		0.90
			Thomisidae	1		0.09
		Unidentified		5		0.45
	Opiliones		Phalangiidae	4		0.36
Chilopoda				1		0.09
Insecta	Collembola	Entomobryoidea		65		5.86
			Sminthuridae	2		0.18
	Coleoptera		Aderidae	1		0.09
			Apionidae	2		0.18
			Buprestidae	1		0.09
			Carabidae	5		0.45
			Cerambycidae	1		0.09
			Chrysomelidae	15		1.35
			Coccinellidae	13		1.17
			Coccinellidae	1	*	0.09
			Curculionidae	4		0.36
			Elateridae	6		0.54
			Lathridiidae	20		1.80
			Melyridae	1		0.09
			Nitidulidae	17		1.53
			Phalacridae	1		0.09
			Scaphidiidae	1		0.09
			Scratiidae	2		0.18
			Staphylinidae	20		1.80
				2	*	0.18
	Dermaptera		Forficulidae	7		0.63
	Diptera		Agromyzidae	99		8.92
			Anthomyiidae	3		0.27
			Anisopodidae	1		0.09
			Aulacigastridae	5		0.45
			Cecidomyiidae	42		3.78
			Chironomidae	4		0.36
			Chloropidae	35		3.15
			Dolichopodidae	3		0.27
			Drosophilidae	11		0.99
			Dryomyzidae	2		0.18
			Empididae	8		0.72
			Epipsocidae	5		0.45
			Ephydridae	3		0.27

Appendix I: Chase Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
			Lauxaniidae	10		0.90
			Lonchopteridae	14		1.26
			Lonchaeidae	1		0.09
			Muscidae	4		0.36
			Mycetophilidae	4		0.36
			Opomyzidae	9		0.81
			Otitidae	1		0.09
			Phoridae	2		0.18
			Piophilidae	1		0.09
			Platypezidae	1		0.09
			Psychodidae	5		0.45
			Sarcophagidae	1		0.09
			Scatophagidae	1		0.09
			Sepsidae	2		0.18
			Sphaeroceridae	2		0.18
			Tachinidae	1		0.09
			Tipulidae	3		0.27
				1	*	0.09
		Unidentified		1		0.09
	Hemiptera	Aphidoidea		203		18.29
			Acanthosomidae	2		0.18
			Cercopidae	7		0.63
			Cicadellidae	27		2.43
			Cimicidae	8		0.72
			Cixiidae	1		0.09
			Coccinellidae	1		0.09
			Coreidae	2		0.18
			Delphacidae	5		0.45
			Lygaeidae	1		0.09
			Melyridae	1		0.09
			Miridae	28		2.52
			Nabiidae	54		4.86
			Scutelleridae	1		0.09
				19		1.71
	Hymenoptera	Chalcidoidea		38		3.42
		Ichneumonoidea		2		0.18
			Braconidae	8		0.72
			Cynipidae	4		0.36
			Ichneumonidae	10		0.90
			Platygasteridae	11		0.99
			Pteromalidae	8		0.72
			Tenthredinidae	1		0.09
				1		0.09
	Lepidoptera	Micropterigoidea		1		0.09
		Pyraloidea		2		0.18
		Tineoidea		5		0.45
			Geometridae	4		0.36

Appendix I: Chase Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
			Pyralidae	2		0.18
			Pyralidae	1	*	0.09
			Satyridae	1		0.09
		Microlepidoptera		6		0.54
	Neuroptera		Chrysopidae	2		0.18
			Chrysopidae	1	*	0.09
	Psocoptera		Ectopsocidae	15		1.35
			Ectopsocidae	3	*	0.27
			Epipsocidae	1		0.09
	Thysanoptera		Phlaethripidae	27		2.43
				1110		100.00

Appendix I: Long Itchington Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
Arachnida	Araneae		Araneidae	3	0.20
			Gnaphosidae	1	0.07
			Tetragnathidae	1	0.07
			Theridiidae	1	0.07
Insecta	Coleoptera		Chrysomelidae	5	0.34
			Coccinellidae	1	0.07
			Lathridiidae	1	0.07
	Diptera		Agromyzidae	3	0.20
			Ceratopogonidae	23	1.55
			Cecidomyiidae	614	41.46
			Chironomidae	194	13.10
			Chloropidae	2	0.14
			Culicidae	3	0.20
			Drosophilidae	1	0.07
			Milichidae	1	0.07
			Muscidae	1	0.07
			Mycetophilidae	17	1.15
			Phoridae	2	0.14
			Psychodidae	361	24.38
			Scatopsidae	1	0.07
			Tipulidae	3	0.20
	Hemiptera	Aphidoidea		14	0.95
			Cercopidae	1	0.07
			Cicadellidae	17	1.15
			Nabiidae	1	0.07
			Psyllidae	3	0.20
	Hymenoptera	Chalcidoidea		3	0.20
		Ichneumonoidea		1	0.07
			Cynipidae	1	0.07
			Ichneumonidae	1	0.07
			Pteromalidae	6	0.41
			Trichogrammitidae	2	0.14
	Lepidoptera	Micropterigoidea		1	0.07
		Microlepidoptera		50	3.38
		Pyraloidea		22	1.49
		Tineoidea		19	1.28
			Arctiidae	1	0.07
			Eriocranidae	1	0.07
			Geometridae	18	1.22
			Nepticulidae	1	0.07
			Noctuidae	6	0.41
			Pyralidae	3	0.20
			Tortricidae	5	0.34
			Yponomeutidae	2	0.14
	Neuroptera		Chrysopidae	45	3.04
			Coniopterygidae	2	0.14
			Hemerobiidae	1	0.07

Appendix I: Long Itchington Wood, Suction Trap Catches

Class	Order	Superfamily	Family	No.	% Total
	Psocoptera		Caecilidae	7	0.47
			Ectopsocidae	6	0.41
	Thysanoptera		Phlaeothripidae	2	0.14
				1481	100.00

Appendix I: Long Itchington Wood, Light Trap Catches

Class	Order	Superfamily	Family	Number		% Total
Arachnida	Araneae		Clubionidae	1		0.05
			Gnaphosidae	3		0.16
			Linyphidae	2		0.11
			Zoridae	1		0.05
	Opiliones		Phalangiidae	105		5.60
Insecta	Coleoptera		Carabidae	1		0.05
			Cantharidae	1	*	0.05
			Cantharidae	4		0.21
			Chrysomelidae	2		0.11
			Coccinellidae	1		0.05
			Curculionidae	1		0.05
			Dytiscidae	1		0.05
			Elateridae	2		0.11
			Haliplidae	1		0.05
			Heteroceridae	1		0.05
			Lathridiidae	2		0.11
			Lymexylidae	1		0.05
			Mycetophagidae	3		0.16
			Scarabaeidae	3		0.16
				1		0.05
	Dermaptera		Forficulidae	3		0.16
			Agromyzidae	5		0.27
			Anthomyiidae	9		0.48
			Anisopodidae	8		0.43
			Calliphoridae	2		0.11
			Camillidae	1		0.05
			Ceratopogonidae	32		1.71
			Cecidomyiidae	28		1.49
			Chironomidae	342		18.24
			Chloropidae	7		0.37
			Dolichopodidae	8		0.43
			Drosophilidae	1		0.05
			Empididae	3		0.16
			Epipsocidae	3		0.16
			Lauxaniidae	1		0.05
			Lonchopteridae	2		0.11
			Muscidae	1		0.05
			Mycetophilidae	55		2.93
			Phoridae	3		0.16
			Psychodidae	45		2.40
			Psilidae	1		0.05
			Sciaridae	2		0.11
			Scatophagidae	3		0.16
			Scatopsidae	1		0.05
			Simulidae	2		0.11
			Syrphidae	11		0.59
			Tachinidae	1		0.05

Appendix I: Long Itchington Wood, Light Trap Catches

Class	Order	Superfamily	Family	Number	% Total
			Tipulidae	107	5.71
			Trichoceridae	1	0.05
	Ephemeroptera		Baetidae	4	0.21
	Hemiptera	Aphidoidea		9	0.48
			Acanthosomidae	1	0.05
			Cercopidae	1	0.05
			Cicadellidae	21	1.12
			Corixidae	3	0.16
			Delphacidae	2	0.11
			Miridae	12	0.64
			Nabiidae	1	0.05
			Psyllidae	1	0.05
	Hymenoptera	Chalcidoidea		2	0.11
		Ichneumonoidea		6	0.32
			Braconidae	6	0.32
			Cynipidae	3	0.16
			Formicidae	4	0.21
			Ichneumonidae	15	0.80
			Proctotrupidae	1	0.05
			Tenthredinidae	1	0.05
	Lepidoptera	Micropterigoidea		1	0.05
		Microlepidoptera		591	31.52
		Pyraloidea		36	1.92
		Tineoidea		16	0.85
			Arctiidae	12	0.64
			Geometridae	89	4.75
			Hepialidae	1	0.05
			Incurvariidae	2	0.11
			Lasiocmpidae	5	0.27
			Lymantriidae	1	0.05
			Nepticulidae	1	0.05
			Noctuidae	123	6.56
			Oecophoridae	1	0.05
			Pyralidae	6	0.32
			Thyatiridae	1	0.05
			Tortricidae	14	0.75
	Neuroptera		Sisyridae	2	0.11
	Trichoptera		Hydropsychidae	7	0.37
			Limnephilidae	45	2.40
			Phyrganeidae	2	0.11
			Philopotamitidae	1	0.05
				1875	100.00

Appendix I: Long Itchington Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
Arachnida	Araneae		Araneidae	17		2.85
			Clusiidae	1		0.17
			Gnaphosidae	8		1.34
			Linyphidae	16		2.68
			Metidae	11		1.85
			Tetragnathidae	10		1.68
			Theridiidae	5		0.84
			Thomisidae	1		0.17
		Unidentified		1		0.17
	Opiliones		Phalangiidae	5		0.84
Crustacea	Isopoda			3		0.50
Diplopoda	Chilopoda			2		0.34
Insecta	Collembola	Entomobryoidea		42		7.05
			Sminthuridae	7		1.17
	Coleoptera		Apionidae	1		0.17
			Carabidae	1		0.17
			Cantharidae	2		0.34
			Chrysomelidae	23		3.86
			Coccinellidae	30		5.03
			Curculionidae	3		0.50
			Erotylidae	1		0.17
			Lathridiidae	25		4.19
			Lymexylidae	1		0.17
			Nitidulidae	38		6.38
			Phalacridae	3		0.50
			Ptilidae	1		0.17
			Staphylinidae	4		0.67
				1	*	0.17
	Dermaptera		Forficulidae	6		1.01
	Diptera		Chloropidae	16		2.68
			Agromyzidae	8		1.34
			Anthomyiidae	2		0.34
			Cecidomyiidae	22		3.69
			Chironomidae	6		1.01
			Chloropidae	34		5.70
			Drosophilidae	2		0.34
			Empididae	3		0.50
			Lauxaniidae	4		0.67
			Lonchopteridae	3		0.50
			Milichidae	2		0.34
			Muscidae	4		0.67
			Mycetophilidae	2		0.34
			Phoridae	3		0.50
			Pipunculidae	1		0.17
			Psychodidae	5		0.84
			Psilidae	1		0.17
			Sarcophagidae	1		0.17

Appendix I: Long Itchington Wood, Sweep Net Catches

Class	Order	Superfamily	Family	No.	*	% Total
			Sciaridae	1		0.17
			Scatophagidae	1		0.17
			Scatopsidae	1		0.17
			Sciomyzidae	1		0.17
			Sphaeroceridae	2		0.34
			Syrphidae	1		0.17
			Tipulidae	8		1.34
	Hemiptera	Aphidoidea		14		2.35
			Cercopidae	3		0.50
			Cicadellidae	30		5.03
			Cimicidae	3		0.50
			Coreidae	3		0.50
			Corixidae	1		0.17
			Delphacidae	1		0.17
			Miridae	18		3.02
			Nabiidae	31		5.20
			Rhopalidae	2		0.34
			Tingidae	1		0.17
				5		0.84
	Hymenoptera	Chalcidoidea		12		2.01
		Ichneumonoidea		1		0.17
		Proctotrupoidea		1		0.17
			Braconidae	10		1.68
			Cynipidae	2		0.34
			Ichneumonidae	6		1.01
			Platygasteridae	3		0.50
			Pteromalidae	3		0.50
			Trigonalidae	1		0.17
	Lepidoptera	Incurvaroidea		5		0.84
		Micropterigoidea		1		0.17
		Pyraloidea		1		0.17
		Tineoidea		7		1.17
			Eriocranidae	3		0.50
			Geometridae	1		0.17
			Geometridae	2	*	0.34
			Tortricidae	3		0.50
				6	*	1.01
	Neuroptera		Chrysopidae	2		0.34
	Orthoptera		Tettigoniidae	5		0.84
	Psocoptera		Ectopsocidae	4		0.67
			Elipsocidae	1		0.17
	Trichoptera		Sericostomatidae	1		0.17
				596		100.00

Appendix II
Correlation Matrices

Table II.i: Pearson Correlation Matrix
Data from all four woodlands together
where n=36 (r>0.28, p<0.1; r>0.33, p<0.05)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Max. temp. Bab.*	1.00															
2	Min. temp. Bab.	0.70	1.00														
3	Soil temp. Bab.	0.81	0.89	1.00													
4	Hrs Sun Bab.	0.60	0.18	0.40	1.00												
5	Rel. Humid. Bab.	-0.25	-0.05	-0.21	-0.41	1.00											
6	Windspeed Bab.	-0.25	0.02	-0.02	-0.06	0.13	1.00										
7	Humid. in wood	-0.35	-0.16	-0.22	-0.30	0.48	0.38	1.00									
8	Ave temp. wood	0.77	0.81	0.77	0.29	0.03	-0.10	-0.22	1.00								
9	Max. temp. wood	0.84	0.75	0.75	0.40	-0.08	-0.30	-0.44	0.91	1.00							
10	Min. temp. wood	0.70	0.79	0.76	0.18	0.05	0.00	-0.07	0.95	0.78	1.00						
11	Bar Pressure Bab.	-0.04	-0.14	-0.11	0.16	-0.27	-0.20	-0.50	-0.27	-0.07	-0.41	1.00					
12	Suction no.1000m-3	0.69	0.69	0.75	0.30	-0.27	-0.14	-0.28	0.63	0.65	0.59	0.00	1.00				
13	Light no. hr-1	0.77	0.80	0.82	0.38	-0.11	-0.09	-0.21	0.88	0.80	0.88	-0.15	0.59	1.00			
14	Sweep no. 1000m-3	0.14	0.27	0.23	-0.06	-0.47	0.15	-0.21	0.01	0.04	0.04	0.06	0.46	0.00	1.00		
15	P. pip 100m-1	-0.09	0.19	0.10	-0.36	0.04	0.12	0.12	0.07	-0.03	0.15	-0.20	0.26	-0.07	0.44	1.00	
16	Myotis 100m-1	-0.12	-0.06	-0.09	0.02	-0.25	0.10	0.04	-0.31	-0.31	-0.18	-0.25	0.02	-0.27	0.51	0.30	1.00

*Bab. means that this data was recorded at Bablake Weather Station, Coventry. Weather data recorded in woodlands were only taken during the night of field work.

Table II.ii: Pearson Correlation Matrix
Data from Tocil Wood
where n=10 (r>0.55, p<0.1; r>0.63, p<0.05)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Cloud. Bab.	1.00																		
2	Max temp. Bab	-0.18	1.00																	
3	Min. temp. Bab.	0.27	0.63	1.00																
4	Soil temp. Bab.	0.02	0.71	0.85	1.00															
5	Rainfall Bab.	-0.32	-0.31	-0.52	-0.38	1.00														
6	Hrs Sun. Bab.	-0.39	0.75	0.05	0.34	-0.11	1.00													
7	Humid. Bab.	-0.22	-0.10	-0.12	-0.20	0.59	-0.09	1.00												
8	Windspeed Bab.	0.40	-0.21	0.09	0.14	-0.26	-0.11	-0.09	1.00											
9	Cloud Cover wood	0.06	-0.48	-0.48	-0.69	0.51	-0.48	0.52	-0.08	1.00										
10	Humid. wood	-0.19	-0.16	-0.33	-0.20	0.88	-0.10	0.50	-0.06	0.50	1.00									
11	Ave. temp. wood	0.21	0.78	0.70	0.53	-0.22	0.34	0.25	-0.05	-0.03	-0.01	1.00								
12	Min. temp. wood	0.30	0.56	0.66	0.47	-0.04	0.04	0.28	0.05	0.19	0.15	0.90	1.00							
13	Max. temp. wood	0.12	0.86	0.71	0.60	-0.43	0.48	0.09	-0.18	-0.23	-0.29	0.93	0.74	1.00						
14	Myotis passes 100m	0.51	-0.44	0.16	0.05	-0.10	-0.58	-0.18	0.77	0.03	0.10	-0.20	0.04	-0.42	1.00					
15	P. pip. passes 100m	0.53	0.10	0.54	0.36	-0.03	-0.29	-0.02	0.50	-0.03	0.13	0.38	0.61	0.12	0.72	1.00				
16	Pressure Bab.	-0.31	0.07	-0.12	0.01	-0.54	0.32	-0.62	-0.24	-0.58	-0.70	-0.42	-0.66	-0.09	-0.36	-0.61	1.00			
17	Suction 1000m-3	0.32	0.63	0.88	0.84	-0.71	0.20	-0.45	0.34	-0.60	-0.42	0.58	0.51	0.62	0.28	0.51	0.06	1.00		
18	Light trap hr-1	0.21	0.83	0.80	0.85	-0.23	0.41	-0.12	0.00	-0.42	-0.03	0.80	0.77	0.79	-0.07	0.49	-0.26	0.77	1.00	
19	Sweep net 1000m-3	0.43	-0.08	0.37	0.39	-0.73	-0.20	-0.73	0.60	-0.52	-0.55	-0.18	-0.14	-0.09	0.62	0.31	0.35	0.65	0.12	1.00

Table II.iii: Pearson Correlation Matrix
Data from Roughknowles Wood
where n=9 (r>0.58, p<0.1; r>0.67, p<0.05)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	Cloud. Bab.	1.00																	
2	Max temp. Bab	-0.20	1.00																
3	Min. temp. Bab.	-0.08	0.73	1.00															
4	Soil temp. Bab.	-0.29	0.84	0.92	1.00														
5	Rainfall Bab.	0.06	-0.56	-0.53	-0.42	1.00													
6	Hrs Sun. Bab.	-0.59	0.50	0.10	0.43	-0.20	1.00												
7	Humid. Bab.	0.77	-0.18	0.10	-0.15	0.09	-0.72	1.00											
8	Windspeed Bab.	-0.19	-0.64	-0.24	-0.37	0.26	-0.25	0.22	1.00										
9	Humid. wood	-0.02	-0.24	0.31	0.17	0.46	-0.45	0.41	0.54	1.00									
10	Ave. temp. wood	-0.06	0.93	0.83	0.86	-0.46	0.20	0.09	-0.56	0.04	1.00								
11	Min. temp. wood	-0.07	0.88	0.84	0.88	-0.32	0.18	0.11	-0.50	0.17	0.99	1.00							
12	Max. temp. wood	-0.03	0.97	0.75	0.82	-0.52	0.34	-0.06	-0.74	-0.20	0.95	0.91	1.00						
13	Myotis passes 100m	-0.09	-0.33	-0.12	-0.09	0.28	0.04	-0.48	-0.08	0.11	-0.40	-0.35	-0.27	1.00					
14	P. pip. passes 100m	0.48	-0.35	0.13	-0.12	-0.04	-0.48	0.18	0.01	0.18	-0.21	-0.19	-0.22	0.53	1.00				
15	Pressure Bab.	0.38	-0.25	-0.09	-0.25	-0.51	-0.05	-0.11	0.02	-0.44	-0.39	-0.48	-0.24	0.38	0.60	1.00			
16	Suction 1000m-3	-0.13	0.68	0.52	0.68	-0.27	0.57	-0.50	-0.72	-0.27	0.55	0.54	0.69	0.39	0.16	0.10	1.00		
17	Light trap hr-1	-0.32	0.85	0.85	0.94	-0.40	0.32	-0.16	-0.50	0.10	0.91	0.91	0.86	-0.16	-0.15	-0.36	0.63	1.00	
18	Sweep net 1000m-3	0.27	-0.10	0.17	0.06	-0.04	-0.22	-0.19	-0.38	0.00	-0.07	-0.06	0.05	0.81	0.81	0.51	0.52	0.07	1.00

Table II.iv: Pearson Correlation Matrix
Data from Chase Wood
where n=10 ($r>0.55$, $p<0.1$; $r>0.63$, $p<0.05$)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	Cloud. Bab.	1.00																	
2	Max temp. Bab	-0.71	1.00																
3	Min. temp. Bab.	-0.10	0.49	1.00															
4	Soil temp. Bab.	-0.46	0.73	0.90	1.00														
5	Rainfall Bab.	0.20	-0.50	-0.09	-0.32	1.00													
6	Hrs Sun. Bab.	-0.53	0.73	0.03	0.32	-0.89	1.00												
7	Humid. Bab.	0.65	-0.48	0.04	-0.34	0.68	-0.71	1.00											
8	Windspeed Bab.	-0.20	-0.04	0.09	0.16	0.42	-0.37	-0.10	1.00										
9	Humid. wood	0.10	-0.54	-0.23	-0.36	0.82	-0.74	0.27	0.67	1.00									
10	Ave. temp. wood	-0.05	0.48	0.88	0.76	-0.10	0.09	0.03	-0.02	-0.18	1.00								
11	Min. temp. wood	-0.21	0.50	0.88	0.78	0.09	-0.01	0.03	0.15	0.01	0.95	1.00							
12	Max. temp. wood	-0.02	0.60	0.74	0.67	-0.43	0.41	-0.03	-0.41	-0.59	0.87	0.73	1.00						
13	Myotis passes 100m	-0.07	-0.10	-0.47	-0.24	-0.30	0.17	-0.39	0.02	-0.13	-0.71	-0.69	-0.51	1.00					
14	P. pip. passes 100m	-0.14	0.28	0.21	0.31	-0.46	0.35	-0.51	0.12	-0.14	0.08	0.07	0.17	0.47	1.00				
15	Pressure Bab.	0.07	-0.03	-0.25	-0.25	-0.21	0.25	0.15	-0.45	-0.43	-0.15	-0.28	0.01	-0.27	-0.73	1.00			
16	Suction 1000m-3	-0.28	0.66	0.40	-0.51	-0.67	0.69	-0.54	-0.22	-0.46	0.44	0.40	0.57	0.08	0.63	-0.26	1.00		
17	Light trap hr-1	-0.47	0.74	0.86	0.91	-0.19	0.30	-0.26	0.24	-0.18	0.85	0.90	0.68	-0.52	0.16	-0.15	0.53	1.00	
18	Sweep net 1000m-3	-0.37	0.25	-0.15	0.11	-0.38	0.39	-0.71	0.19	0.03	-0.17	-0.08	-0.23	0.47	0.38	-0.21	0.59	0.13	1.00

Table II.v: Pearson Correlation Matrix
Data from Long Itchington Wood
where n=9 ($r>0.58$, $p<0.1$; $r>0.67$, $p<0.05$)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Cloud. Bab.	1.00																		
2	Max temp. Bab	0.21	1.00																	
3	Min. temp. Bab.	0.30	0.85	1.00																
4	Soil temp. Bab.	0.22	0.95	0.93	1.00															
5	Rainfall Bab.	0.20	-0.40	0.02	-0.21	1.00														
6	Hrs Sun. Bab.	-0.04	0.39	0.20	0.47	-0.12	1.00													
7	Humid. Bab.	0.34	-0.32	0.07	-0.16	0.82	-0.28	1.00												
8	Windspeed Bab.	0.41	-0.23	0.04	-0.02	0.52	0.09	0.74	1.00											
9	Cloud Cover wood	-0.26	-0.68	-0.35	-0.48	0.48	-0.24	0.36	0.38	1.00										
10	Humid. wood	-0.41	-0.59	-0.40	-0.51	0.46	-0.26	0.58	0.42	0.36	1.00									
11	Ave. temp. wood	0.32	0.83	0.99	0.93	0.05	0.27	0.02	0.06	-0.29	-0.46	1.00								
12	Min. temp. wood	0.24	0.71	0.95	0.85	0.18	0.18	0.14	0.16	-0.10	-0.32	0.97	1.00							
13	Max. temp. wood	0.43	0.92	0.93	0.93	-0.15	0.30	-0.13	-0.06	-0.60	-0.56	0.93	0.84	1.00						
14	Myotis passes 100m	-0.28	0.18	0.08	0.15	-0.41	-0.13	-0.36	-0.38	0.28	-0.44	0.08	0.09	-0.06	1.00					
15	P. pip. passes 100m	-0.11	0.40	0.32	0.37	-0.44	-0.21	-0.34	-0.18	0.10	-0.41	0.33	0.36	0.26	0.75	1.00				
16	Pressure Bab.	-0.01	-0.09	-0.50	-0.24	-0.32	0.22	-0.31	-0.04	-0.31	0.01	-0.47	-0.54	-0.23	-0.19	0.05	1.00			
17	Sweep net 1000m-3	0.42	0.43	0.24	0.35	-0.53	-0.06	-0.12	0.14	-0.23	-0.47	0.20	0.13	0.29	0.50	0.64	0.20	1.00		
18	Suction 1000m-3	0.15	0.90	0.90	0.96	-0.13	0.42	-0.03	0.00	-0.38	-0.42	0.88	0.82	0.83	0.27	0.36	-0.33	0.38	1.00	
19	Light trap hr-1	0.36	0.69	0.88	0.83	0.24	0.27	0.16	0.16	-0.06	-0.47	0.92	0.93	0.79	0.22	0.40	-0.40	0.23	0.83	1.00

Table II.vi: Pearson Correlation Matrix
Data from Tocil Wood (windspeed, Myotis passes and insect numbers in sweep net)
where n=9 (r>0.58, p<0.1; r>0.67, p<0.05)

		1	2	3	4	5	6
1	Windspeed Bab.	1.00					
2	Pressure Bab.	-0.37	1.00				
3	Sweep net no. Dense Vegetation 1	0.14	-0.59	1.00			
4	Sweep net no. Edge	0.67	0.16	0.00	1.00		
5	Myotis passes Dense Vegetation 1	0.69	-0.21	-0.01	0.79	1.00	
6	Myotis passes Edge	0.80	-0.41	0.30	0.36	0.50	1.00

Table II.vii: Pearson Correlation Matrix
Data from Long Itchington Wood (windspeed, Myotis passes and insect numbers in sweep net)
where n=9 (r>0.58, p<0.1; r>0.67, p<0.05)

		1	2	3	4	5	6
1	Windspeed Bab.	1.00					
2	Pressure Bab.	-0.04	1.00				
3	Sweep net no. Clear-cut	-0.26	-0.19	1.00			
4	Sweep net no. Dense vegetation	0.06	0.34	-0.70	1.00		
5	Myotis passes Clear-cut	0.82	0.04	-0.15	0.34	1.00	
6	Myotis passes Dense vegetation	-0.61	0.18	-0.06	-0.05	-0.59	1.00

Appendix III
Batmodels BASIC code

Batmodel 1

```
 10 REM BAT MODEL VERSION 1.2
 20 REM
 30 REM STATIONARY OBSERVER
 40 REM
 50 REM BATS MOVING IN CIRCLES
 60 REM
 70 REM 15TH MARCH 1997
100 REM
110 REM **********************
120 REM
130 REM BSPEED = BAT SPEED (LINEAR) M/S
140 BSPEED=4
150 REM NSPEED = NIAMH'S SPEED M/S
160 NSPEED =0
170 REM OBSRAD = OBSERVATION RADIUS M
180 OBSRAD=17.32
190 REM TRANSECT = LENGTH OF TRANSECT M
200 TRANSECT=0
210 REM BATNUM = NUMBER OF BATS
220 INPUT "ENTER NUMBER OF BATS ",BATNUM
230 REM BATRAD = RADIUS OF BAT FLIGHT CIRCLES
240 INPUT "ENTER RADIUS OF BAT FLIGHT CIRCLES",BATRAD
250 REM WOODX = LENGTH OF SIDE OF WOOD ALONG X AXIS M
260 WOODX=(OBSRAD*2)+(BATRAD*2)
270 REM WOODY = LENGTH OF SIDE OF WOOD ALONG Y AXIS M
280 WOODY=(OBSRAD*2)+(BATRAD*2)+TRANSECT
290 REM NPOS IS NIAMH'S POSITION
300 DIM NPOS(2)
310 NPOS(1)=OBSRAD+BATRAD
320 NPOS(2)=OBSRAD+BATRAD
330 REM BATOMEGA = BAT ANGULAR VELOCITY RAD/S
340 BATOMEGA=BSPEED/BATRAD
350 REM ITER = ITERATIONS PER SECOND
360 INPUT "ENTER ITERATIONS PER SECOND ",ITER
370 REM INITIALISE COUNTERS TO ZERO
380 REM OBSPASS IS NUMBER OF BAT PASSES OBSERVED
390 OBSPASS=0
400 REM REALPASS IS NUMBER OF ACTUAL BAT PASSES
410 REALPASS=0
420 REM DIFPASS IS NUMBER OF PASSES BY DIFFERENT BATS
430 DIFPASS=0
440 REM PRESENT IS NUMBER OF BATS WITHIN OBSERVATION RANGE
450 PRESENT=0
460 REM LAST IS NUMBER OF BATS WITHIN RANGE LAST TIME STEP
470 LAST=0
480 REM SET UP ARRAYS FOR FINDING OUT CLOSEST BATS
490 DIM DISTANCE(BATNUM)
500 DIM CLOSE1(2)
510 DIM CLOSE2(2)
530 CLOSE1(2)=10000
550 CLOSE2(2)=10000
560 LCLOSE1=99999
570 LCLOSE2=99999
580 REM GO TO SUBROUTINE SETUP
```

```
 590 GOSUB 830
 600 INPUT "ENTER MODEL RUN TIME IN SECONDS ",SEC
 610 REM
 620 REM ************************
 630 REM
 640 FOR J=1 TO (SEC*ITER)
 650 REM GOSUB CHECK
 660 GOSUB 1310
 670 REM GOSUB MOVE BATS
 680 GOSUB 2010
 690 NEXT
 700 PRINT "OBSPASS IS"
 710 PRINT OBSPASS
 720 PRINT "REALPASS IS"
 730 PRINT REALPASS
 740 PRINT "DIFPASS IS"
 750 PRINT DIFPASS
 760 DENSITY=BATNUM/(WOODX*WOODY)
 770 PRINT "DENSITY OF BATS (BATS PER SQUARE METER) IS"
 780 PRINT DENSITY
 790 END
 800 REM
 810 REM ***************************
 820 REM
 830 REM SUBROUTINE SETUP
 840 DIM BATS(8,BATNUM)
 850 REM ARRAY:
 860 REM FIRST ELEMENT - X COORD OF BAT'S ORIGIN
 870 REM SECOND ELEMENT - Y COORD OF BAT'S ORIGIN
 880 REM THIRD ELEMENT - ANGLE OF LINE BETWEEN BAT AND ITS ORIGIN AND
 890 REM                 X AXIS
 900 REM FOURTH ELEMENT - BAT'S X COORD
 910 REM FIFTH ELEMENT - BAT'S Y COORD
 920 REM SIXTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT IS
 930 REM                 IN OBSERVATION CIRCLE
 940 REM SEVENTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT WAS
 950 REM                   IN OBSERVATION LAST CYCLE
 960 REM EIGHTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT HAS
 970 REM                  BEEN OBSERVED BEFORE
 980 REM
 990 FOR I=1 TO BATNUM
1000 REM
1010 REM ASSIGN RANDOM INITIAL VALUES TO FIRST THREE ELEMENTS OF ARRAY
1020 BATS(1,I)=RND(WOODX)
1030 BATS(2,I)=RND(WOODY)
1040 X=RND(1)
1050 BATS(3,I)=X*2*PI
1060 REM CALCULATE VALUES OF FOURTH AND FIFTH ELEMENTS OF ARRAY
1070 BATS(4,I)=(BATRAD*(COS(BATS(3,I))))+BATS(1,I)
1080 IF BATS(4,I)>WOODX THEN
1090 BATS(4,I)=WOODX
1100 ENDIF
1110 IF BATS(4,I)<0 THEN
1120 BATS(4,I)=0
1130 ENDIF
1140 BATS(5,I)=(BATRAD*(SIN(BATS(3,I))))+BATS(2,I)
```

```
1150 IF BATS(5,I)>WOODY THEN
1160 BATS(5,I)=WOODY
1170 ENDIF
1180 IF BATS(5,I)<0 THEN
1190 BATS(5,I)=0
1200 ENDIF
1210 REM
1220 REM INITIALISE FLAGS TO FALSE (0)
1230 BATS(6,I)=0
1240 BATS(7,I)=0
1250 BATS(8,I)=0
1260 NEXT
1270 RETURN
1280 REM
1290 REM *************************
1300 REM
1310 REM SUBROUTINE CHECK
1320 REM CHECKS IF BATS WITHIN OBSERVATION CIRCLE
1330 REM OBSPASS = NUMBER OF OBSERVED BAT PASSES
1340 REM REALPASS = ACTUAL NUMBER OF BAT PASSES
1350 REM DIFPASS = NUMBER OF PASSES BY DIFFERENT BATS
1360 REM PRESENT = NUMBER OF BATS IN OBSERVATION CIRCLE
1370 REM DISTANCE = DISTANCE BETWEEN NIAMH AND BAT
1380 CLOSE1(1)=10000
1390 CLOSE2(1)=10000
1400 FOR I=1 TO BATNUM
1410 DISTANCE(I)=(((BATS(4,I)-NPOS(1))^2)+((BATS(5,I)-NPOS(2))^2))^0.5
1420 IF DISTANCE(I)<OBSRAD THEN
1430 BATS(6,I)=1
1440 ELSE
1450 BATS(6,I)=0
1460 ENDIF
1470 IF BATS(6,I)=1 AND BATS(7,I)=0 THEN
1480 PRESENT=PRESENT+1
1490 REALPASS=REALPASS+1
1500 IF BATS(8,I)=0 THEN
1510 DIFPASS=DIFPASS+1
1520 BATS(8,I)=1
1530 ENDIF
1540 ENDIF
1550 IF DISTANCE(I)<CLOSE1(1) THEN
1560 CLOSE2(1)=CLOSE1(1)
1570 CLOSE2(2)=CLOSE1(2)
1580 CLOSE1(1)=DISTANCE(I)
1590 CLOSE1(2)=I
1600 ELSE
1610 IF DISTANCE(I)<CLOSE2(1) THEN
1620 CLOSE2(1)=DISTANCE(I)
1630 CLOSE2(2)=I
1640 ENDIF
1650 ENDIF
1660 IF BATS(6,I)=0 AND BATS(7,I)=1 THEN
1670 PRESENT=PRESENT-1
1680 ENDIF
1690 NEXT
```

```
1700 IF PRESENT=1 THEN
1710 IF (BATS(6,CLOSE1(2))=1 AND BATS(7,CLOSE1(2))=0) THEN
1720 OBSPASS=OBSPASS+1
1730 ENDIF
1740 ENDIF
1750 IF PRESENT>=2 THEN
1760 IF LAST=0 THEN
1770 IF (BATS(6,CLOSE1(2))=1 AND BATS(7,CLOSE1(2))=0) THEN
1780 OBSPASS=OBSPASS+1
1790 ENDIF
1800 IF (BATS(6,CLOSE2(2))=1 AND BATS(7,CLOSE2(2))=0) THEN
1810 OBSPASS=OBSPASS+1
1820 ENDIF
1830 ELSE
1840 IF ((CLOSE1(2)<>LCLOSE1) AND (CLOSE1(2)<>LCLOSE2)) OR (BATS(6,CLOSE1(2))=1
AND BATS(7,CLOSE1(2))=0) THEN
1850 OBSPASS=OBSPASS+1
1860 ELSE
1870 IF ((CLOSE2(2)<>LCLOSE1) AND (CLOSE2(2)<>LCLOSE2)) OR (BATS(6,CLOSE2(2))=1
AND BATS(7,CLOSE2(2))=0) THEN
1880 OBSPASS=OBSPASS+1
1890 ENDIF
1900 ENDIF
1910 ENDIF
1920 ENDIF
1930 LAST=PRESENT
1940 FOR I=1 TO BATNUM: BATS(7,I)=BATS(6,I): NEXT
1950 LCLOSE1=CLOSE1(2)
1960 LCLOSE2=CLOSE2(2)
1970 RETURN
1980 REM
1990 REM **********************
2000 REM
2010 REM SUBROUTINE MOVE BATS
2020 FOR I=1 TO BATNUM
2030 BATS(3,I)=BATS(3,I)+(BATOMEGA/ITER)
2040 REM CALCULATE NEW X,Y COORDS
2050 BATS(4,I)=(BATRAD*(COS(BATS(3,I))))+BATS(1,I)
2060 IF BATS(4,I)>WOODX THEN
2070 BATS(4,I)=WOODX
2080 ENDIF
2090 IF BATS(4,I)<0 THEN
2100 BATS(4,I)=0
2110 ENDIF
2120 BATS(5,I)=(BATRAD*(SIN(BATS(3,I))))+BATS(2,I)
2130 IF BATS(5,I)>WOODY THEN
2140 BATS(5,I)=WOODY
2150 ENDIF
2160 IF BATS(5,I)<0 THEN
2170 BATS(5,I)=0
2180 ENDIF
2190 NEXT
2200 RETURN
2210 REM
2220 REM **********************
2230 REM
```

Batmodel 2

```
 10 REM BAT MODEL VERSION 2.3
 20 REM
 30 REM STATIONARY OBSERVER
 40 REM
 50 REM BATS MOVING IN RANDOM WALK
 60 REM
 70 REM FINISHED MODEL
 80 REM
 90 REM ************************
100 REM
110 REM BSPEED = BAT SPEED (LINEAR) M/S
120 BSPEED=4
130 REM NSPEED = NIAMH'S SPEED M/S
140 NSPEED =0
150 REM NPOS IS NIAMH'S POSITION
160 DIM NPOS(2)
170 NPOS(1)=39
180 NPOS(2)=39
190 REM OBSRAD = OBSERVATION RADIUS M
200 OBSRAD=17.32
210 REM TRANSECT = LENGTH OF TRANSECT M
220 TRANSECT=0
230 REM BATNUM = NUMBER OF BATS
240 INPUT "ENTER NUMBER OF BATS ",BATNUM
250 REM WOOD = LENGTH OF SIDE OF WOOD (WOOD IS SQUARE) M
260 WOOD=78
270 REM ITER = ITERATIONS PER SECOND
280 INPUT "ENTER ITERATIONS PER SECOND ",ITER
290 REM SET UP ARRAYS FOR FINDING OUT CLOSEST BAT
300 DIM DISTANCE(BATNUM)
310 DIM CLOSE1(2)
320 DIM CLOSE2(2)
330 CLOSE1(2)=10000
340 CLOSE2(2)=10000
350 LCLOSE1=99999
360 LCLOSE2=99999
370 REM INITIALISE COUNTERS TO ZERO
380 REM OBSPASS IS THE NUMBER OF OBSERVED BAT PASSES
390 OBSPASS=0
400 REM REALPASS IF THE NUMBER OF ACTUAL BAT PASSES
410 REALPASS=0
420 REM DIFPASS IS THE NUMBER OF PASSES BY DIFFERENT BATS
430 DIFPASS=0
440 REM PRESENT IS THE NUMBER OF BATS CURRENTLY IN RANGE
450 PRESENT=0
460 REM LAST IS THE NUMBER OF BATS THAT WERE IN RANGE LAST TIME STEP
470 LAST=0
480 REM GO TO SUBROUTINE SETUP
490 GOSUB 720
500 INPUT "ENTER MODEL RUN TIME IN SECONDS ",SEC
510 REM
520 REM ************************
530 REM
540 FOR J=1 TO (SEC*ITER)
```

```
 550 REM GOSUB CHECK
 560 GOSUB 950
 570 REM GOSUB MOVE BATS
 580 GOSUB 1640
 590 NEXT
 600 PRINT "OBSPASS IS"
 610 PRINT OBSPASS
 620 PRINT "REALPASS IS"
 630 PRINT REALPASS
 640 PRINT "DIFPASS IS"
 650 PRINT DIFPASS
 660 DENSITY=BATNUM/(WOOD^2)
 670 PRINT "BAT DENSITY PER SQUARE METER IS"
 680 PRINT DENSITY
 690 END
 700 REM **********************
 710 REM
 720 REM SUBROUTINE SETUP
 730 DIM BATS(5,BATNUM)
 740 REM ARRAY:
 750 REM FIRST ELEMENT - BAT'S X COORD
 760 REM SECOND ELEMENT - BAT'S Y COORD
 770 REM THIRD ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT IS
 780 REM                 IN OBSERVATION CIRCLE
 790 REM FOURTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT WAS
 800 REM                   IN OBSERVATION LAST CYCLE
 810 REM FIFTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT HAS
 820 REM                  BEEN OBSERVED BEFORE
 830 REM
 840 FOR I=1 TO BATNUM
 850 REM
 860 REM ASSIGN RANDOM INITAL COORDS TO EACH BAT
 870 BATS(1,I)=WOOD*RND(1)
 880 BATS(2,I)=WOOD*RND(1)
 890 REM INITIALISE FLAGS TO FALSE (0)
 900 BATS(3,I)=0
 910 BATS(4,I)=0
 920 BATS(5,I)=0
 930 NEXT
 940 RETURN
 950 REM SUBROUTINE CHECK
 960 REM CHECKS IF BATS WITHIN OBSERVATION CIRCLE
 970 REM OBSPASS = NUMBER OF OBSERVED BAT PASSES
 980 REM REALPASS = ACTUAL NUMBER OF BAT PASSES
 990 REM DIFPASS = NUMBER OF PASSES BY DIFFERENT BATS
1000 REM PRESENT = NUMBER OF BATS IN OBSERVATION CIRCLE
1010 REM DISTANCE = DISTANCE BETWEEN NIAMH AND BAT
1020 CLOSE1(1)=10000
1030 CLOSE2(1)=10000
1040 FOR I=1 TO BATNUM
1050 DISTANCE(I)=(((BATS(1,I)-NPOS(1))^2)+((BATS(2,I)-NPOS(2))^2))^0.5
1060 IF DISTANCE(I)<OBSRAD THEN
1070 BATS(3,I)=1
1080 ELSE
1090 BATS(3,I)=0
1100 ENDIF
1110 IF BATS(3,I)=1 AND BATS(4,I)=0 THEN
1120 PRESENT=PRESENT+1
```

```
1130 REALPASS=REALPASS+1
1140 IF BATS(5,I)=0 THEN
1150 DIFPASS=DIFPASS+1
1160 BATS(5,I)=1
1170 ENDIF
1180 ENDIF
1190 IF BATS(3,I)=0 AND BATS(4,I)=1 THEN
1200 PRESENT=PRESENT-1
1210 ENDIF
1220 IF DISTANCE(I)<CLOSE1(1) THEN
1230 CLOSE2(1)=CLOSE1(1)
1240 CLOSE2(2)=CLOSE1(2)
1250 CLOSE1(1)=DISTANCE(I)
1260 CLOSE1(2)=I
1270 ELSE
1280 IF DISTANCE(I)<CLOSE2(1) THEN
1290 CLOSE2(1)=DISTANCE(I)
1300 CLOSE2(2)=I
1310 ENDIF
1320 ENDIF
1330 NEXT
1340 IF PRESENT=1 THEN
1350 IF (BATS(3,CLOSE1(2))=1 AND BATS(4,CLOSE1(2))=0) THEN
1360 OBSPASS=OBSPASS+1
1370 ENDIF
1380 ENDIF
1390 IF PRESENT>=2 THEN
1400 IF LAST=0 THEN
1410 IF (BATS(3,CLOSE1(2))=1 AND BATS(4,CLOSE1(2))=0) THEN
1420 OBSPASS=OBSPASS+1
1430 ENDIF
1440 IF (BATS(3,CLOSE2(2))=1 AND BATS(4,CLOSE2(2))=0) THEN
1450 OBSPASS=OBSPASS+1
1460 ENDIF
1470 ELSE
1480 IF ((CLOSE1(2)<>LCLOSE1) AND (CLOSE1(2)<>LCLOSE2)) OR (BATS(3,CLOSE1(2))=1
AND BATS(4,CLOSE1(2))=0) THEN
1490 OBSPASS=OBSPASS+1
1500 ELSE
1510 IF ((CLOSE2(2)<>LCLOSE1) AND (CLOSE2(2)<>LCLOSE2)) OR (BATS(3,CLOSE2(2))=1
AND BATS(4,CLOSE2(2))=0) THEN
1520 OBSPASS=OBSPASS+1
1530 ENDIF
1540 ENDIF
1550 ENDIF
1560 ENDIF
1570 LAST=PRESENT
1580 FOR I=1 TO BATNUM
1590 BATS(4,I)=BATS(3,I)
1600 NEXT
1610 LCLOSE1=CLOSE1(2)
1620 LCLOSE2=CLOSE2(2)
1630 RETURN
```

```
1640 REM SUBROUTINE MOVE BATS
1650 FOR I=1 TO BATNUM
1660 THETA=2*PI*RND(1)
1670 BATS(1,I)=BATS(1,I)+((BSPEED/ITER)*(COS(THETA)))
1680 IF BATS(1,I)>WOOD THEN
1690 BATS(1,I)=WOOD
1700 ENDIF
1710 IF BATS(1,I)<0 THEN
1720 BATS(1,I)=0
1730 ENDIF
1740 BATS(2,I)=BATS(2,I)+((BSPEED/ITER)*(SIN(THETA)))
1750 IF BATS(2,I)>WOOD THEN
1760 BATS(2,I)=WOOD
1770 ENDIF
1780 IF BATS(2,I)<0 THEN
1790 BATS(2,I)=0
1800 ENDIF
1810 NEXT
1820 RETURN
```

Batmodel 3

```
 10 REM BAT MODEL VERSION 3.2
 20 REM
 30 REM MOVING OBSERVER
 40 REM
 50 REM BATS MOVING IN CIRCLES
 60 REM
 70 REM FINISHED MODEL
 80 REM
 90 REM
100 REM **********************
110 REM
120 REM BSPEED = BAT SPEED (LINEAR) M/S
130 BSPEED=4
140 REM NSPEED = NIAMH'S SPEED M/S
150 NSPEED =1
160 REM OBSRAD = OBSERVATION RADIUS M
170 OBSRAD=17.32
180 REM TRANSECT = LENGTH OF TRANSECT M
190 TRANSECT=200
200 REM BATNUM = NUMBER OF BATS
210 INPUT "ENTER NUMBER OF BATS ",BATNUM
220 REM BATRAD = RADIUS OF BAT FLIGHT CIRCLES
230 INPUT "ENTER RADIUS OF BAT FLIGHT CIRCLES",BATRAD
240 REM WOODX = LENGTH OF SIDE OF WOOD ALONG X AXIS M
250 WOODX=(OBSRAD*2)+(BATRAD*2)
260 REM WOODY = LENGTH OF SIDE OF WOOD ALONG Y AXIS M
270 WOODY=(OBSRAD*2)+(BATRAD*2)+TRANSECT
280 REM NPOS IS NIAMH'S POSITION
290 DIM NPOS(2)
300 NPOS(1)=OBSRAD+BATRAD
310 NPOS(2)=OBSRAD+BATRAD
320 REM BATOMEGA = BAT ANGULAR VELOCITY RAD/S
330 BATOMEGA=BSPEED/BATRAD
340 REM ITER = ITERATIONS PER SECOND
350 INPUT "ENTER ITERATIONS PER SECOND ",ITER
360 REM INITIALISE COUNTERS TO ZERO
370 REM OBSPASS IS NUMBER OF BAT PASSES OBSERVED
380 OBSPASS=0
390 REM REALPASS IS NUMBER OF ACTUAL BAT PASSES
400 REALPASS=0
410 REM DIFPASS IS NUMBER OF PASSES BY DIFFERENT BATS
420 DIFPASS=0
430 REM PRESENT IS NUMBER OF BATS WITHIN OBSERVATION RANGE
440 PRESENT=0
450 REM LAST IS NUMBER OF BATS WITHIN RANGE LAST TIME STEP
460 LAST=0
470 REM SET UP ARRAYS FOR FINDING OUT CLOSEST BATS
480 DIM DISTANCE(BATNUM)
490 DIM CLOSE1(2)
500 DIM CLOSE2(2)
510 CLOSE1(2)=10000
520 CLOSE2(2)=10000
530 LCLOSE1=99999
540 LCLOSE2=99999
```

```
550 REM GO TO SUBROUTINE SETUP
560 GOSUB 830
570 REM SEC=MODEL RUN TIME IN SECONDS
580 SEC=TRANSECT/NSPEED
590 REM
600 REM ************************
610 REM
620 FOR J=1 TO (SEC*ITER)
630 REM GOSUB CHECK
640 GOSUB 1310
650 REM GOSUB MOVE BATS
660 GOSUB 2010
670 REM GOSUB MOVE OBSERVER
680 GOSUB 2240
690 NEXT
700 PRINT "OBSPASS IS"
710 PRINT OBSPASS
720 PRINT "REALPASS IS"
730 PRINT REALPASS
740 PRINT "DIFPASS IS"
750 PRINT DIFPASS
760 DENSITY=BATNUM/(WOODX*WOODY)
770 PRINT "DENSITY OF BATS (BATS PER SQUARE METER) IS"
780 PRINT DENSITY
790 END
800 REM
810 REM ***************************
820 REM
830 REM SUBROUTINE SETUP
840 DIM BATS(8,BATNUM)
850 REM ARRAY:
860 REM FIRST ELEMENT - X COORD OF BAT'S ORIGIN
870 REM SECOND ELEMENT - Y COORD OF BAT'S ORIGIN
880 REM THIRD ELEMENT - ANGLE OF LINE BETWEEN BAT AND ITS ORIGIN AND
890 REM                 X AXIS
900 REM FOURTH ELEMENT - BAT'S X COORD
910 REM FIFTH ELEMENT - BAT'S Y COORD
920 REM SIXTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT IS
930 REM                 IN OBSERVATION CIRCLE
940 REM SEVENTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT WAS
950 REM                   IN OBSERVATION LAST CYCLE
960 REM EIGHTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT HAS
970 REM                  BEEN OBSERVED BEFORE
980 REM
990 FOR I=1 TO BATNUM
1000 REM
1010 REM ASSIGN RANDOM INITIAL VALUES TO FIRST THREE ELEMENTS OF ARRAY
1020 BATS(1,I)=RND(WOODX)
1030 BATS(2,I)=RND(WOODY)
1040 X=RND(1)
1050 BATS(3,I)=X*2*PI
1060 REM CALCULATE VALUES OF FOURTH AND FIFTH ELEMENTS OF ARRAY
1070 BATS(4,I)=(BATRAD*(COS(BATS(3,I))))+BATS(1,I)
1080 IF BATS(4,I)>WOODX THEN
1090 BATS(4,I)=WOODX
```

```
1100 ENDIF
1110 IF BATS(4,I)<0 THEN
1120 BATS(4,I)=0
1130 ENDIF
1140 BATS(5,I)=(BATRAD*(SIN(BATS(3,I))))+BATS(2,I)
1150 IF BATS(5,I)>WOODY THEN
1160 BATS(5,I)=WOODY
1170 ENDIF
1180 IF BATS(5,I)<0 THEN
1190 BATS(5,I)=0
1200 ENDIF
1210 REM
1220 REM INITIALISE FLAGS TO FALSE (0)
1230 BATS(6,I)=0
1240 BATS(7,I)=0
1250 BATS(8,I)=0
1260 NEXT
1270 RETURN
1280 REM
1290 REM ************************
1300 REM
1310 REM SUBROUTINE CHECK
1320 REM CHECKS IF BATS WITHIN OBSERVATION CIRCLE
1330 REM OBSPASS = NUMBER OF OBSERVED BAT PASSES
1340 REM REALPASS = ACTUAL NUMBER OF BAT PASSES
1350 REM DIFPASS = NUMBER OF PASSES BY DIFFERENT BATS
1360 REM PRESENT = NUMBER OF BATS IN OBSERVATION CIRCLE
1370 REM DISTANCE = DISTANCE BETWEEN NIAMH AND BAT
1380 CLOSE1(1)=10000
1390 CLOSE2(1)=10000
1400 FOR I=1 TO BATNUM
1410 DISTANCE(I)=(((BATS(4,I)-NPOS(1))^2)+((BATS(5,I)-NPOS(2))^2))^0.5
1420 IF DISTANCE(I)<OBSRAD THEN
1430 BATS(6,I)=1
1440 ELSE
1450 BATS(6,I)=0
1460 ENDIF
1470 IF BATS(6,I)=1 AND BATS(7,I)=0 THEN
1480 PRESENT=PRESENT+1
1490 REALPASS=REALPASS+1
1500 IF BATS(8,I)=0 THEN
1510 DIFPASS=DIFPASS+1
1520 BATS(8,I)=1
1530 ENDIF
1540 ENDIF
1550 IF DISTANCE(I)<CLOSE1(1) THEN
1560 CLOSE2(1)=CLOSE1(1)
1570 CLOSE2(2)=CLOSE1(2)
1580 CLOSE1(1)=DISTANCE(I)
1590 CLOSE1(2)=I
1600 ELSE
1610 IF DISTANCE(I)<CLOSE2(1) THEN
1620 CLOSE2(1)=DISTANCE(I)
1630 CLOSE2(2)=I
1640 ENDIF
1650 ENDIF
```

```
1660 IF BATS(6,I)=0 AND BATS(7,I)=1 THEN
1670 PRESENT=PRESENT-1
1680 ENDIF
1690 NEXT
1700 IF PRESENT=1 THEN
1710 IF (BATS(6,CLOSE1(2))=1 AND BATS(7,CLOSE1(2))=0) THEN
1720 OBSPASS=OBSPASS+1
1730 ENDIF
1740 ENDIF
1750 IF PRESENT>=2 THEN
1760 IF LAST=0 THEN
1770 IF (BATS(6,CLOSE1(2))=1 AND BATS(7,CLOSE1(2))=0) THEN
1780 OBSPASS=OBSPASS+1
1790 ENDIF
1800 IF (BATS(6,CLOSE2(2))=1 AND BATS(7,CLOSE2(2))=0) THEN
1810 OBSPASS=OBSPASS+1
1820 ENDIF
1830 ELSE
1840 IF ((CLOSE1(2)<>LCLOSE1) AND (CLOSE1(2)<>LCLOSE2)) OR (BATS(6,CLOSE1(2))=1
AND BATS(7,CLOSE1(2))=0) THEN
1850 OBSPASS=OBSPASS+1
1860 ELSE
1870 IF ((CLOSE2(2)<>LCLOSE1) AND (CLOSE2(2)<>LCLOSE2)) OR (BATS(6,CLOSE2(2))=1
AND BATS(7,CLOSE2(2))=0) THEN
1880 OBSPASS=OBSPASS+1
1890 ENDIF
1900 ENDIF
1910 ENDIF
1920 ENDIF
1930 LAST=PRESENT
1940 FOR I=1 TO BATNUM: BATS(7,I)=BATS(6,I): NEXT
1950 LCLOSE1=CLOSE1(2)
1960 LCLOSE2=CLOSE2(2)
1970 RETURN
1980 REM
1990 REM **********************
2000 REM
2010 REM SUBROUTINE MOVE BATS
2020 FOR I=1 TO BATNUM
2030 BATS(3,I)=BATS(3,I)+(BATOMEGA/ITER)
2040 REM CALCULATE NEW X,Y COORDS
2050 BATS(4,I)=(BATRAD*(COS(BATS(3,I))))+BATS(1,I)
2060 IF BATS(4,I)>WOODX THEN
2070 BATS(4,I)=WOODX
2080 ENDIF
2090 IF BATS(4,I)<0 THEN
2100 BATS(4,I)=0
2110 ENDIF
2120 BATS(5,I)=(BATRAD*(SIN(BATS(3,I))))+BATS(2,I)
2130 IF BATS(5,I)>WOODY THEN
2140 BATS(5,I)=WOODY
2150 ENDIF
2160 IF BATS(5,I)<0 THEN
2170 BATS(5,I)=0
2180 ENDIF
2190 NEXT
2200 RETURN
2210 REM
2220 REM **********************
2230 REM
2240 REM SUBROUTINE MOVE OBSERVER
2250 NPOS(2)=NPOS(2)+NSPEED/ITER
2260 RETURN
```

```
580 REM
590 FOR J=1 TO (SEC*ITER)
600 REM GOSUB CHECK
610 GOSUB 1020
620 REM GOSUB MOVE BATS
630 GOSUB 1710
640 REM GOSUB MOVE OBSERVER
650 GOSUB 1900
660 NEXT
670 PRINT "OBSPASS IS"
680 PRINT OBSPASS
690 PRINT "REALPASS IS"
700 PRINT REALPASS
710 PRINT "DIFPASS IS"
720 PRINT DIFPASS
730 DENSITY=BATNUM/(WOODX*WOODY)
740 PRINT "BAT DENSITY PER SQUARE METER IS"
750 PRINT DENSITY
760 END
770 REM **********************
780 REM
790 REM SUBROUTINE SETUP
800 DIM BATS(5,BATNUM)
810 REM ARRAY:
820 REM FIRST ELEMENT - BAT'S X COORD
830 REM SECOND ELEMENT - BAT'S Y COORD
840 REM THIRD ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT IS
850 REM                 IN OBSERVATION CIRCLE
860 REM FOURTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT WAS
870 REM                   IN OBSERVATION LAST CYCLE
880 REM FIFTH ELEMENT - FLAG (1=TRUE, 0=FALSE) INDICATING WHETHER BAT HAS
890 REM                  BEEN OBSERVED BEFORE
900 REM
910 FOR I=1 TO BATNUM
920 REM
930 REM ASSIGN RANDOM INITAL COORDS TO EACH BAT
940 BATS(1,I)=WOODX*RND(1)
950 BATS(2,I)=WOODY*RND(1)
960 REM INITIALISE FLAGS TO FALSE (0)
970 BATS(3,I)=0
980 BATS(4,I)=0
990 BATS(5,I)=0
1000 NEXT
1010 RETURN
1020 REM SUBROUTINE CHECK
1030 REM CHECKS IF BATS WITHIN OBSERVATION CIRCLE
1040 REM OBSPASS = NUMBER OF OBSERVED BAT PASSES
1050 REM REALPASS = ACTUAL NUMBER OF BAT PASSES
1060 REM DIFPASS = NUMBER OF PASSES BY DIFFERENT BATS
1070 REM PRESENT = NUMBER OF BATS IN OBSERVATION CIRCLE
1080 REM DISTANCE = DISTANCE BETWEEN NIAMH AND BAT
1090 CLOSE1(1)=10000
1100 CLOSE2(1)=10000
1110 FOR I=1 TO BATNUM
1120 DISTANCE(I)=(((BATS(1,I)-NPOS(1))^2)+((BATS(2,I)-NPOS(2))^2))^0.5
1130 IF DISTANCE(I)<OBSRAD THEN
```

```
1140 BATS(3,I)=1
1150 ELSE
1160 BATS(3,I)=0
1170 ENDIF
1180 IF BATS(3,I)=1 AND BATS(4,I)=0 THEN
1190 PRESENT=PRESENT+1
1200 REALPASS=REALPASS+1
1210 IF BATS(5,I)=0 THEN
1220 DIFPASS=DIFPASS+1
1230 BATS(5,I)=1
1240 ENDIF
1250 ENDIF
1260 IF BATS(3,I)=0 AND BATS(4,I)=1 THEN
1270 PRESENT=PRESENT-1
1280 ENDIF
1290 IF DISTANCE(I)<CLOSE1(1) THEN
1300 CLOSE2(1)=CLOSE1(1)
1310 CLOSE2(2)=CLOSE1(2)
1320 CLOSE1(1)=DISTANCE(I)
1330 CLOSE1(2)=I
1340 ELSE
1350 IF DISTANCE(I)<CLOSE2(1) THEN
1360 CLOSE2(1)=DISTANCE(I)
1370 CLOSE2(2)=I
1380 ENDIF
1390 ENDIF
1400 NEXT
1410 IF PRESENT=1 THEN
1420 IF (BATS(3,CLOSE1(2))=1 AND BATS(4,CLOSE1(2))=0) THEN
1430 OBSPASS=OBSPASS+1
1440 ENDIF
1450 ENDIF
1460 IF PRESENT>=2 THEN
1470 IF LAST=0 THEN
1480 IF (BATS(3,CLOSE1(2))=1 AND BATS(4,CLOSE1(2))=0) THEN
1490 OBSPASS=OBSPASS+1
1500 ENDIF
1510 IF (BATS(3,CLOSE2(2))=1 AND BATS(4,CLOSE2(2))=0) THEN
1520 OBSPASS=OBSPASS+1
1530 ENDIF
1540 ELSE
1550 IF ((CLOSE1(2)<>LCLOSE1) AND (CLOSE1(2)<>LCLOSE2)) OR (BATS(3,CLOSE1(2))=1
AND BATS(4,CLOSE1(2))=0) THEN
1560 OBSPASS=OBSPASS+1
1570 ELSE
1580 IF ((CLOSE2(2)<>LCLOSE1) AND (CLOSE2(2)<>LCLOSE2)) OR (BATS(3,CLOSE2(2))=1
AND BATS(4,CLOSE2(2))=0) THEN
1590 OBSPASS=OBSPASS+1
1600 ENDIF
1610 ENDIF
1620 ENDIF
1630 ENDIF
1640 LAST=PRESENT
```

```
1650 FOR I=1 TO BATNUM
1660 BATS(4,I)=BATS(3,I)
1670 NEXT
1680 LCLOSE1=CLOSE1(2)
1690 LCLOSE2=CLOSE2(2)
1700 RETURN
1710 REM SUBROUTINE MOVE BATS
1720 FOR I=1 TO BATNUM
1730 THETA=2*PI*RND(1)
1740 BATS(1,I)=BATS(1,I)+((BSPEED/ITER)*(COS(THETA)))
1750 IF BATS(1,I)>WOODX THEN
1760 BATS(1,I)=WOODX
1770 ENDIF
1780 IF BATS(1,I)<0 THEN
1790 BATS(1,I)=0
1800 ENDIF
1810 BATS(2,I)=BATS(2,I)+((BSPEED/ITER)*(SIN(THETA)))
1820 IF BATS(2,I)>WOODY THEN
1830 BATS(2,I)=WOODY
1840 ENDIF
1850 IF BATS(2,I)<0 THEN
1860 BATS(2,I)=0
1870 ENDIF
1880 NEXT
1890 RETURN
1900 REM GOSUB MOVE OBSERVER
1910 NPOS(2)=NPOS(2)+NSPEED/ITER
1920 RETURN
```

ABSTRACTS

Poster presented at the 10th International Bat Research Conference, Boston, USA, August 1995.

PREY AVAILABILITY AND HABITAT UTILIZATION BY BATS IN ENGLISH DECIDUOUS WOODLANDS. N. Roche and P. Elliott. University of Warwick, Coventry, England, UK.

Deciduous woodland is important foraging habitat for bats in Europe. However, little work has been carried out to determine utilization of component sub-habitats and the influence of insect abundance. Woodlands of differing size and similar sub-habitats were chosen as sites for this study. Deciduous woodlands are complicated habitats with many variables influencing bat and bat-prey abundance. Four study sites were divided into sub-habitats such as areas of coppice, wetland, rides and glades. Bat abundance in spring and early summer was estimated in these sub-habitats by walking transects of known length and observing bats using ultrasonic bat detectors and torchlight. Prey availability was studied during the night using a suction trap, a light trap and a sweep net. Variations in weather conditions were recorded at each site with a remote data logger. Field work each month was conducted at the same stage of the lunar cycle. The study examined the use of woodlands by bats and determined the sub-habitat preferences during a single season. Preliminary findings suggest that long rides within dense woodland are used more than other, more abundant, sub-habitats such as areas of coppice, by *Myotis* spp. However, this pattern of use may change during the season.

Oral presentation at the VIIth European Bat Research Symposium, Eindhoven, The Netherlands, August 1996.

DIFFERENTIAL USE OF STRUCTURAL FEATURES IN DECIDUOUS WOODLAND BY FORAGING BATS IN CENTRAL ENGLAND. N. Roche and P. Elliott. University of Warwick, Coventry, England

Fragmented deciduous woodlands form an important part of the English landscape. Management practices within these sites can affect the abundance and diversity of animals found there, Four small mature woods in central England were studied for bat abundance from April to September 1995. Relative activity was estimated using bat detectors while walking line transects several times throughout a night. Transects covered various structural features within woods, such as glades, rides, edges, coppiced areas etc. Results were analysed to reveal differences in the use of these features relative to availability. Between the four woodlands studied, no difference was found in overall bat abundance along transects. However, activity was often concentrated in certain areas. During most of the season small natural clearings were used more than expected by *Myotis* species and pipistrelles (*Pipistrellus pipistrellus*). Woodland edges were avoided by all species

throughout the season. Areas of dense vegetation were often avoided by pipistrelles. Insect availability was measured using several methods and was significantly correlated with relative bat numbers within woods. The effects of weather conditions such as humidity and temperature were also considered. Results from this study have practical implications for bat conservation when considering ways to improve bat-friendly areas in a predominantly agricultural landscape.

Oral presentation at the VIIth European Bat Research Symposium, Eindhoven, The Netherlands, August 1996.

DETERMINING THE LOCATION OF BAT ROOSTS AND BAT ROOST DENSITIES USING A QUESTIONNAIRE SURVEY. P. Elliott and N. Roche, University of Warwick, Coventry, England.

Locating bat roosts sites and establishing their density in an area can be a difficult and time-consuming task. A novel approach to this problem is described: the use of a questionnaire survey to locate bat roosts. The questionnaire was designed to obtain as much valuable information as possible, while maximising response rates. It was distributed to all inhabited buildings in a 25km2 rural study area in central England. There was a good response rate (47%) and, with follow-up investigations, the survey revealed a high density of previously unrecorded roosts. The technique can dramatically increase roost records and complements other methods, such as bat detector survey work. Questionnaires are a cost effective way to locate roosts and at the same time raise public awareness of bat conservation.